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Integrative analysis of ecosystem processes in the littoral zone of lower Chesapeake Bay: A modeling study of the Goodwin Islands National Estuarine Research Reserve

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INTEGRATIVE ANALYSIS OF ECOSYSTEM PROCESSES IN THE LITTORAL
ZONE OF LOWER CHESAPEAKE BAY: A MODELING STUDY OF THE GOODWIN
ISLANDS NATIONAL ESTUARINE RESEARCH RESERVE

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirement for the Degree of

Doctor of Philosophy

by

Christopher P. Buzzelli

1996

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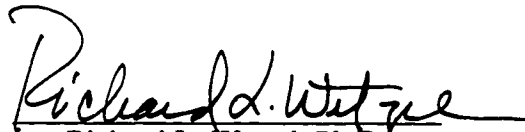
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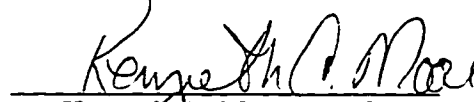
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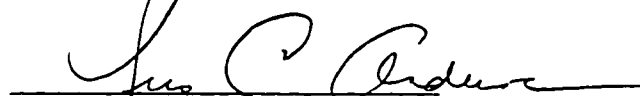
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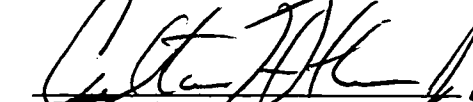
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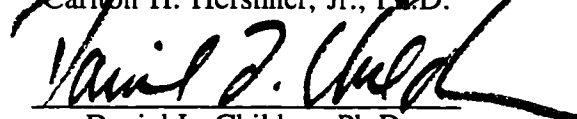

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DEDICATION

This dissertation is dedicated to all of the soccer players, coaches, and fans in the world.

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ABSTRACT

Approximately 40% of the bottom of Chesapeake Bay is less than 2.0 m in depth and many of these broad shoal environments are bordered by wetlands. The vegetated and nonvegetated subtidal and intertidal environment is a dynamic mosaic of highly productive estuarine habitats linked by the exchange of waterborne materials. This study developed simulation models of primary production and material exchange for four littoral zone habitats of the Goodwin Islands National Estuarine Research Reserve (NERR) in lower Chesapeake Bay. Field studies were conducted to determine the sediment biogeochemical and biomass characteristics of sandy shoal, seagrass, silt-mud, and marsh habitats. Ecological models were developed for each habitat based upon their position and ecological characteristics. The models simulate the dynamics of phytoplankton, particulate and dissolved organic carbon, dissolved inorganic nitrogen, sediment microalgae, *Zostera marina*, and *Spartina alterniflora*. Following sensitivity analysis and validation the models were used to estimate annual primary production, nitrogen processes, and material exchange. The net annual rate of phytoplankton production was 66.0, sediment microalgae ranged 101-169, *Zostera marina* community production was approximately 350 gC m⁻² yr⁻¹, and *Spartina alterniflora* shoots and root-rhizomes produced 1150 gC m⁻² yr⁻¹ (gC m⁻² yr⁻¹). Nitrogen uptake was in excess of demand in phytoplankton while the reverse was true for the macrophytes. The marsh habitat accounted for 43% of the total annual primary production for the ecosystem despite being the smallest habitat while the largest habitat (nonvegetated subtidal) required 52% of the total ecosystem nitrogen demand. All four habitats imported phytoplankton, particulate organic carbon, and dissolved inorganic nitrogen annually. While the intertidal habitats imported dissolved organic carbon the subtidal habitats showed net annual export. These models were developed to assess ecosystem structure, function, and change in the littoral zone of Chesapeake Bay. Ecosystem structure was assessed through field research and model development. Ecosystem function was assessed by using the model to generate annual producer, habitat, and ecosystem carbon and nitrogen budgets. The model is currently being used to investigate the interactive effects of water quality, primary production, and habitat composition in order to assess potential change in the estuary.

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Section 1

PROJECT OVERVIEW

INTRODUCTION & BACKGROUND

Natural systems function over a continuum of spatial and temporal scales (Fig. 1). Between the extreme of the microscales (molecular, tissue) and the macroscales (watershed, landscape) are a range of mesoscales where local events (e.g. patch dynamics) interact with coarser scale processes generating variable environmental patterns on human scales of time and space (Holling 1992). There are suites of dynamic processes that predominate at each spatio-temporal level of organization (O'Neill et al. 1989). Because there are principle driving factors at each scale there is also environmental patchiness at each scale (Levin 1992). The field of landscape ecology seeks to understand the nature of spatial heterogeneity including dynamic mosaics, the exchanges across heterogeneous boundaries within the mosaics, the effects of spatial pattern upon biotic and abiotic processes, and the potential management of heterogeneity (Turner and Gardner 1991). Landscape ecology is concerned with the structure, function, and the potential change of the heterogeneous system of interest (Turner and Gardner 1991).

Estuaries are dynamic coastal landscapes where biogeochemical patterns are generated under the influence of hydrodynamic control (Childers et al. 1994). Within the estuary there are similar ecological processes and patterns that are evident among the landscape, watershed, ecosystem, and habitat scales (Fig. 1). Similarities include the effects of tidal prism and excursion, salinity, temperature, and irradiance upon primary productivity, carbon transfer, and nutrient cycling. The estuarine water column connects and integrates the components of the spatially heterogeneous mosaic (Childers et al. 1994) and primary productivity is closely associated with physical and chemical processes through feedback mechanisms (Costanza et al. 1990). In the Chesapeake Bay landscape, 40% of the subtidal bottom is less than 2.0 m in depth (Spinner 1969), many of these areas are or have been vegetated by submersed macrophytes (Orth and Moore 1984), and long stretches of shoal environments are bordered by fringing marshes. Within the estuarine

flanks are patches of sand, seagrass, mudflat, and marsh habitats that create an explicit mosaic and the connectivity among the patches depends upon their sizes, shapes, and configuration (Wiens et al. 1993; Vorosmarty and Loder 1994). Many local areas of lower Chesapeake Bay possess these characteristic habitats and perhaps their structure, function, and change provide insight into dynamics at coarser scales.

Ecological modeling can be used to describe spatial phenomena, predict temporal changes, integrate between scales, and investigate cause and effect in the system of interest (Sklar and Costanza 1989). The development and utilization of ecosystem models involves a compromise between realism, precision, and generality (Costanza et al. 1990). It is difficult for any one model or model series to optimize all three of these attributes and usually two of the characteristics are emphasized at the expense of the third. Modeling requires just enough detail (precision) to produce observed patterns (realism) without totally sacrificing applicability (generality; Levin 1992). Mechanistic modeling can be used to organize information and identify missing data (Christian and Wetzel 1991), to explore mechanisms and relate fine-scale data to coarse scale patterns (Levin 1992), and to perform hindcasting or forecasting (Costanza et al. 1990).

The primary objective of this doctoral research project was to utilize mechanistic modeling and the basic tenets of landscape ecology to analyze habitat and ecosystem primary production and material flux in the littoral zone of the Goodwin Islands National Estuarine Research Reserve (NERR) in the lower Chesapeake Bay. The littoral zone is defined as the area between the -2.0 m depth contour (relative to mean low water) and the high tide limit above the high marsh habitat. Within the littoral zone of the Goodwin Islands NERR is a mosaic of sand, seagrass, mudflat, and marsh habitats that is characteristic of many areas of the lower, polyhaline reaches of Chesapeake Bay. The goals of this study were to (1) develop an integrative research framework with which to analyze coastal zone ecosystem dynamics, and, (2) describe and investigate the emergent

ecosystem properties of the the Goodwin Islands NERR. This study utilized field data collection and geographic information systems to determine the structure of the Goodwin Islands ecosystem. Models were developed based upon the habitat distribution within the littoral zone in order to investigate habitat and ecosystem function. These models are currently being deployed to analyze potential change in the littoral zone of the Goodwin Islands and the results of this study will help better understand the role of the littoral zone in the Chesapeake Bay landscape.

This dissertation is divided into six sections including this project overview (Section 1), three research chapters, a summary/synthesis, and an appendix section. Section 2 characterizes the subtidal and intertidal habitats of the Goodwin Islands through field and laboratory efforts. The habitat configuration and composition provided in Section 2 served as a basis for the development and calibration of a series of habitat simulation models that are presented in Section 3. The models developed in Section 3 were used in Section 4 to generate producer, habitat, and ecosystem carbon and nitrogen budgets and to assess material flux in the littoral zone of the Goodwin Islands NERR. A chapter summary, information synthesis, and project analysis is included in Section 5 and the appendix (Section 6) contains the diagrams, equation code, and documentation for the seagrass and marsh habitat models. Section 6 provides specific details of model set-up and mathematics.

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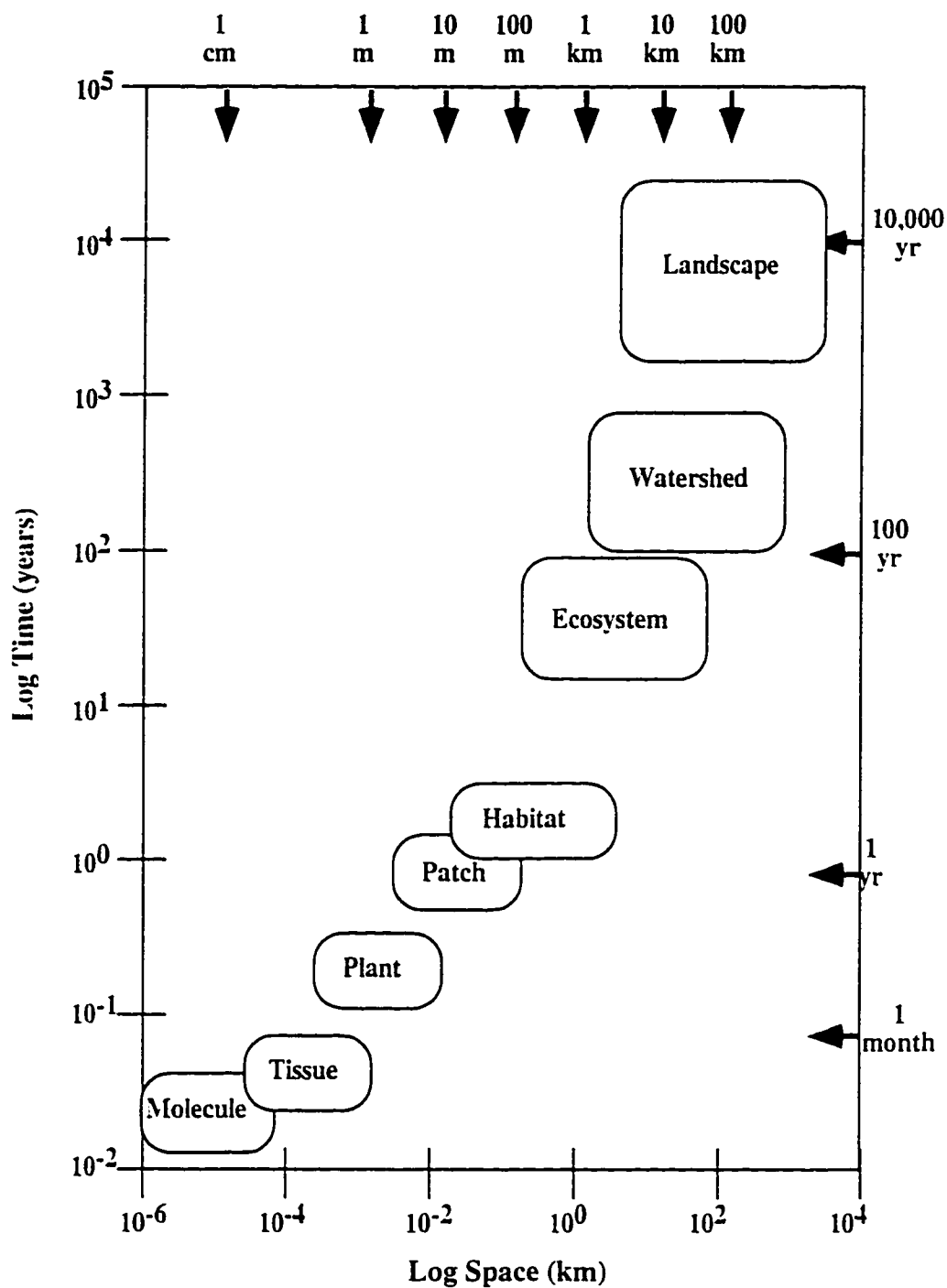


Figure 1. Logarithmic space and time scales for the analysis of ecological phenomena. Adapted from Holling (1992) to reflect estuarine patterns.

Section 2

AN ECOLOGICAL CHARACTERIZATION OF A SEAGRASS AND SALT MARSH
COMPLEX OF LOWER CHESAPEAKE BAY: THE GOODWIN ISLANDS NATIONAL
ESTUARINE RESEARCH RESERVE*

*To be submitted to Estuaries

ABSTRACT

The fringing environments of lower Chesapeake Bay include sandy shoals, seagrass meadows, intertidal mud flats, and estuarine marshes. One way to characterize the different habitats is to analyze patterns of sediment biogeochemistry and biomass. This study provides a biogeochemical characterization that is an essential prelude to spatial ecosystem modeling of habitat processes and patterns in lower Chesapeake Bay. Nearshore water column properties were determined bi-weekly and cores were collected seasonally to determine water column and sediment carbon and nitrogen properties of nonvegetated and vegetated subtidal and intertidal habitats of the Goodwin Islands National Estuarine Research Reserve (NERR). The seasonal distribution and abundance of *Zostera marina* and *Spartina alterniflora* were also determined. The marsh sediments differed significantly from those of the subtidal and nearshore habitats in terms of sediment carbon and nitrogen characteristics. Phytoplankton biomass displayed some seasonality related to riverine discharge but sediment microalgal biomass did not vary spatially or seasonally. Vegetation in both subtidal and intertidal habitats displayed seasonal patterns in coverage and biomass that were consistent with other Atlantic estuarine ecosystems. The information on habitat composition, distribution, and ecological characteristics are being used as background information to develop mathematical models of habitat and ecosystem material production and exchange.

INTRODUCTION

In Chesapeake Bay approximately 40% of the submerged bottom is less than 2.0 m in depth and many of these broad shoal environments are bordered by fringing wetlands (Spinner, 1969). While seagrass distribution historically extended to this two meter depth, seagrasses currently survive only to approximately one meter due to long term changes in water quality (Dennison et al., 1993; Orth and Moore, 1984). Because many of the intertidal wetlands abut steep mainland slopes the fringing marshes of Chesapeake Bay do not migrate landward and are eroding from wave effects at the edges, subsurface peat breakdown, and internal ponding (Finklestein and Hardaway, 1988; Stevenson et al., 1988). The combination of open water, partially vegetated shoals, intertidal mud flats, high and low marshes, and forested and agricultural upland creates a mosaic of estuarine habitats that are linked by the dynamic exchange of waterborne materials (Correll et al., 1992). These various habitats are organized along physical gradients such as sediment elevation and each possesses ecological characteristics that reflect both the external environmental parameters as well as the resource requirements of the constituents (Sand-Jensen and Borum, 1991).

Phytoplankton, sediment microalgae, seagrasses, and marsh vegetation are the main primary producers in Atlantic coast estuaries (de Jonge and Colijn, 1994; Mallin, 1994; Pinckney and Zingmark, 1993; Roman et al., 1990; Schubauer and Hopkinson, 1984; Wetzel and Penhale, 1983). Annual patterns in phytoplankton biomass reflect seasonal changes in meteorological and hydrodynamic forces and in many estuaries are the predominant source of aquatic primary production (de Jonge and Colijn, 1994; Mallin, 1994; Malone et al., 1988). The maximum phytoplankton biomass in the York River, Virginia usually occurs in the winter and early spring (Batuik et al., 1992; Malone et al., 1988). Autotrophic microalgal communities are found in subtidal sediments (de Jonge and Colijn, 1994; Rizzo et al., 1992), seagrass meadow sediments (Moncreiff et al., 1992).

intertidal sand and mud flats (Gould and Gallagher, 1990; Pinckney and Zingmark, 1993), and intertidal marsh sediments (Pinckney and Zingmark, 1993; Sullivan and Moncreiff, 1988). Seagrass meadows are areas of intense primary and secondary production and are considered to be indicators of ecosystem water quality (Dennison et al., 1993; Fredette et al., 1990; Wetzel and Penhale, 1983). In Chesapeake Bay seagrass meadows experience maximum growth and biomass from April to July, massive leaf loss from July to September, and a short lived secondary spurt in growth and biomass throughout the fall and early winter (Orth and Moore, 1986). *Spartina alterniflora* is the dominant macrophyte of Atlantic coastal marshes, survives within a narrow elevation range between mean and high tide levels, and experiences maximum biomass in the late summer (Gross et al., 1991; McKee and W. H. Patrick, 1988; Mendelssohn, 1973).

An understanding of the sediment biogeochemical and biomass properties of the ecosystem components helps provide a starting point for more detailed inquiries into the material linkages among the habitats and the surrounding environment. Surprisingly few studies have included a variety of habitats or primary producers in the analysis of estuarine ecosystem or landscape processes and patterns (Childers et al., 1993; Correll et al., 1992; Pinckney and Zingmark, 1993; Roman et al., 1990; Thorne-Miller et al., 1983). Interestingly, no such studies exist for the lower Chesapeake Bay where several different habitats can be found over a comparatively short horizontal distance between the 2.0 m depth and the upland. Microalgae, *Zostera marina*, and *Spartina alterniflora* are three of the principle primary producers found in lower Chesapeake Bay and the biomass properties of these phototrophs can be used to help characterize the habitats, and therefore the ecosystem, in which they are located.

This is a summary of field efforts and comparative data analysis conducted in support of spatial ecosystem modeling of the littoral zone environments of lower Chesapeake Bay (Buzzelli Sections 3 and 4). The first objective of this study was to

determine the sediment biogeochemical and biomass characteristics of a series of complex habitats organized over a gradient of elevation in a local littoral zone ecosystem. The second objective of this study was to compare and contrast some of the characteristics of the lower Chesapeake Bay littoral zone environments with those of other estuarine ecosystems. Comparative data analysis was used to analyze biogeochemical patterns over geographically separated ecosystems and to assemble data sets for model calibration and validation. This study is significant because it provided the information on the size and composition of a series of habitats that was essential to the development of simulation models that are used to analyze ecosystem dynamics and analyze environmental change in the littoral zone of lower Chesapeake Bay.

METHODS

Study Site

The Goodwin Islands NERR is located at the mouth of the York River in lower Chesapeake Bay (37° 12' 46" N, 76° 23' 46" W; Fig 1). The islands are owned by the College of William and Mary and are managed by the Chesapeake Bay National Estuarine Research Reserve System in Virginia (CBNERRS-VA) of the National Oceanic and Atmospheric Administration (NOAA). The research reserve includes the islands and a buffer zone that extends out to the -2.0 m depth contour (MLW: US Dept. Of Commerce, 1991). There is an extensive subtidal sandy shoal approximately 640 hectares (ha) in size of which 120 ha are vegetated primarily by *Zostera marina* L. although there is some *Ruppia maritima* L. nearshore (Fig. 2). There is a nonvegetated nearshore environment comprised of finer sediments and mudflats that surrounds about 75 ha of intertidal marshes vegetated primarily by *Spartina alterniflora* Loisel although there are some higher marsh patches of *Distichlis spicata* (L.) Greene and *Juncus roemerianus* Scheele (Fig. 2). Near the elevation of maximum tidal excursion there is a salt bush habitat that includes the *Iva*

Figure 1. The location of the Goodwin Islands National Estuarine Research Reserve in the lower York River, Virginia. The Chesapeake Bay and the Goodwin Islands study site are depicted in the left and right insets, respectively.

York River and Mobjack Bay

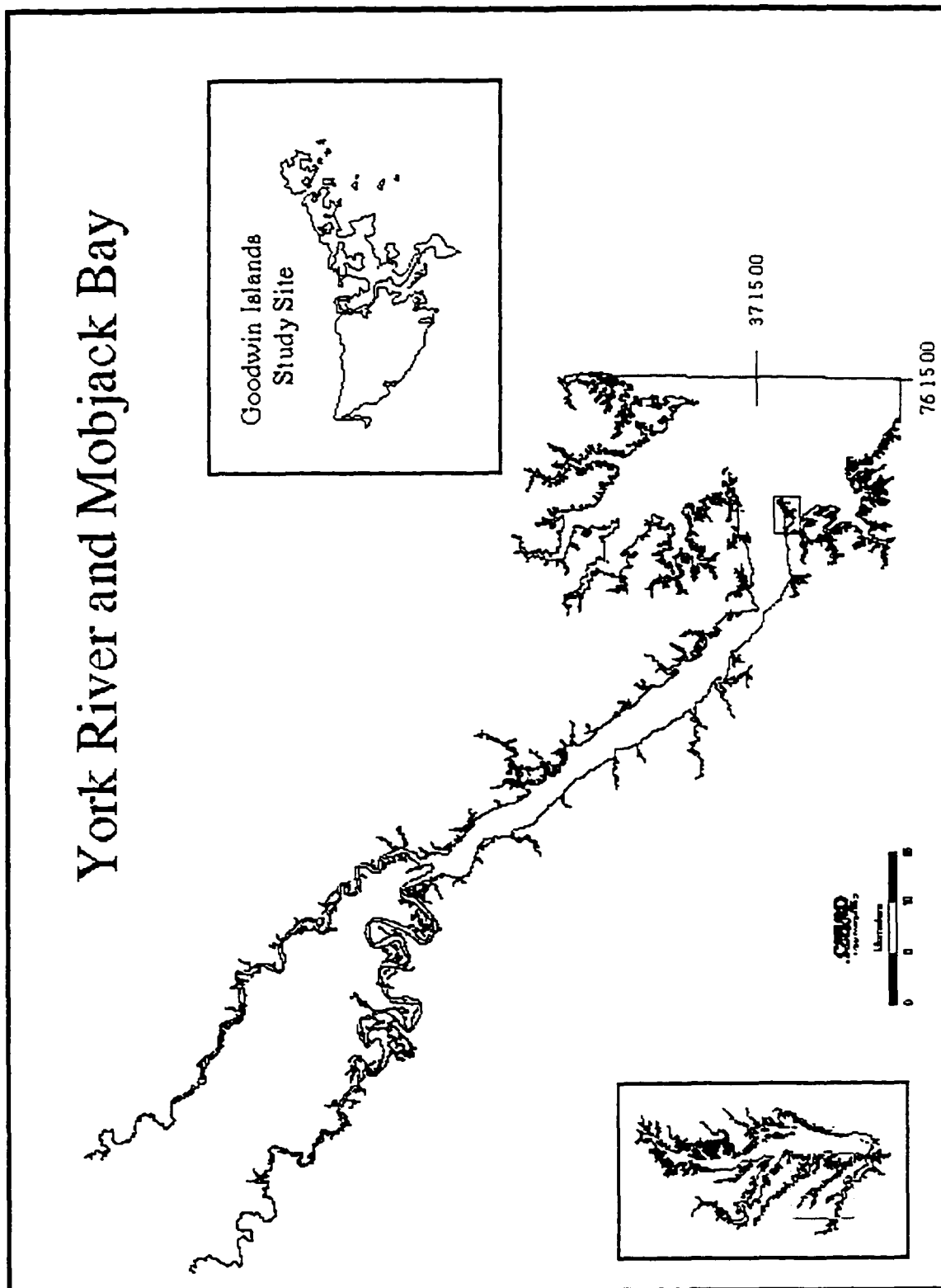
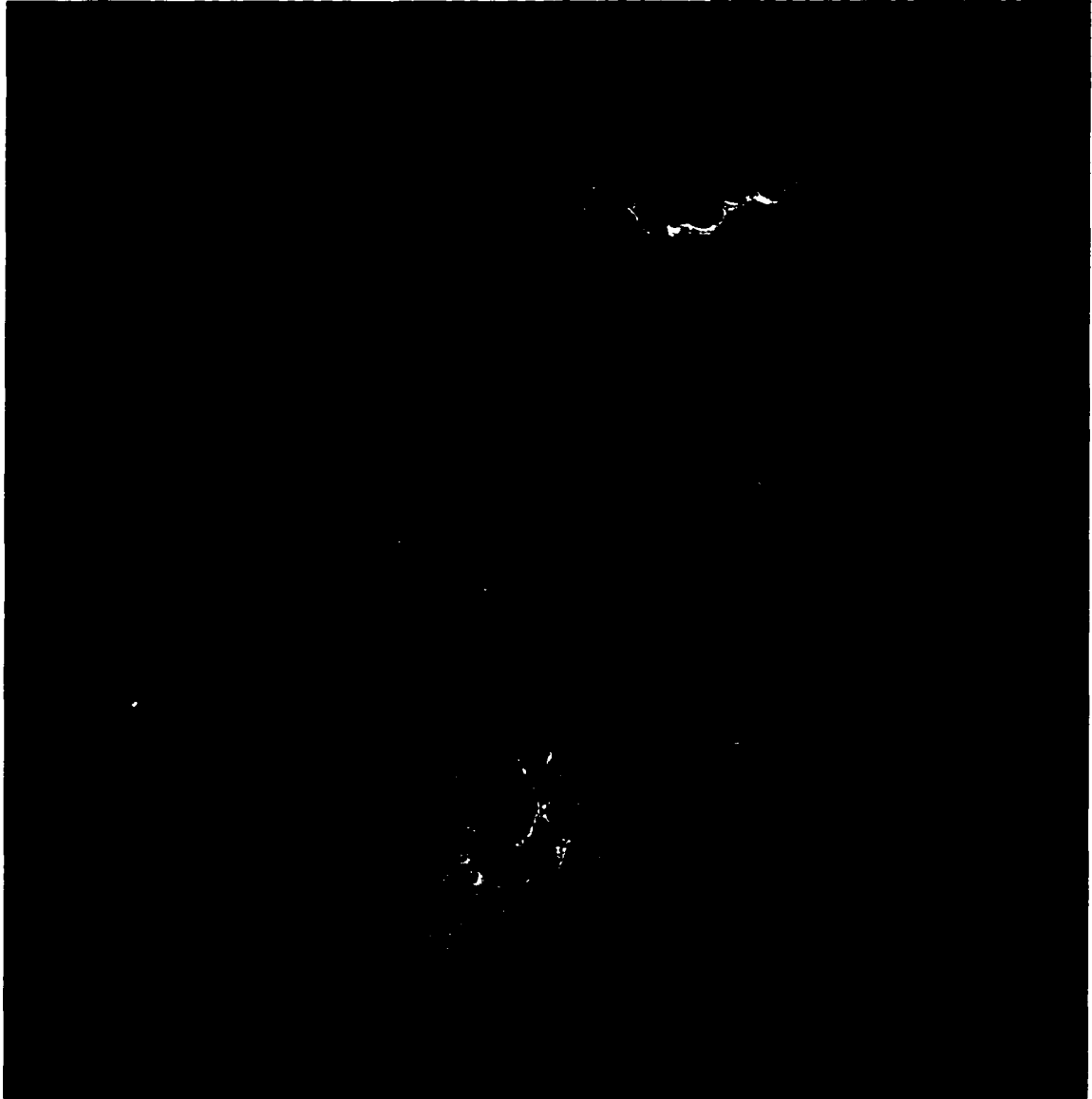


Figure 2. Aerial photograph of a section of the Goodwin Islands NERR. This photo was taken at 5400 feet in May 1995 using a Hasselblat 70 mm camera system.



frutescens L. and *Baccharis halimifolia* L. and the largest island has a small area of maritime forest and upland vegetated by *Quercus rubra* L. (red oak), *Pinus taeda* L. (loblolly pine), *Nyssa sylvatica* Marshall (black gum), and *Populus deltoides* Marshall (cottonwood; J. Perry, pers. comm).

Sampling Design

To establish locations for the sediment core collection within the Goodwin Islands NERR this study employed a randomized sampling design stratified by habitat. Four primary littoral habitats (strata) for the Goodwin Islands NERR were designated as nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT; Figs 2 and 3). An area along the south (bay) side of the islands that measured approximately 200 m X 1200 m from marsh to offshore and encompassed parts of all four habitats from -2.36 m depth to approximately +0.36 m elevation relative to mean sea level (MSL) was divided into 260 numbered grids. This study area also included a platform array used to perform time series analysis of water quality and seagrasses metabolism (Moore et al., 1994). Random numbers (1-260) were drawn to assign locations within each of the strata for the collection of sediment cores. Because the marsh habitat is the most spatially heterogeneous a systematic random sampling design was adopted within the marsh to investigate spatial vegetative and sediment properties along a transect that traversed the entire portion of marsh. The marsh transect sampling locations also served as ground truth points for the determination of horizontal and vertical position (x, y, z) using Global Positioning Systems (GPS).

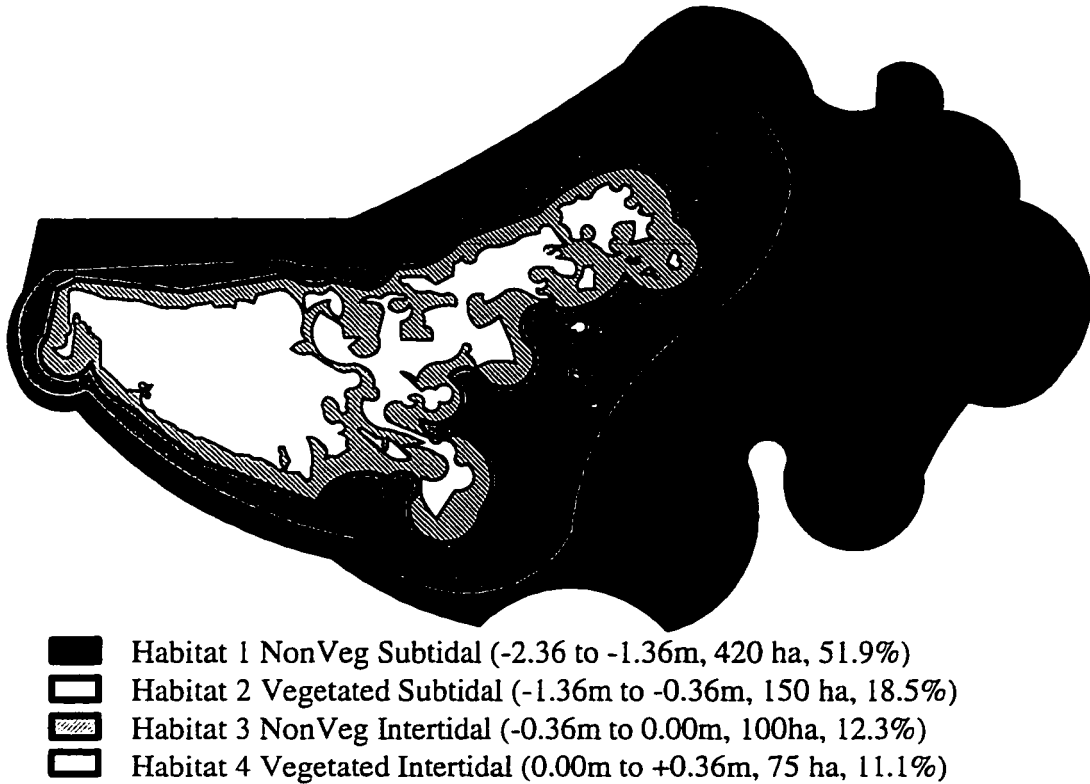
Sample Collection and Processing

Subtidal and Nearshore Sediments

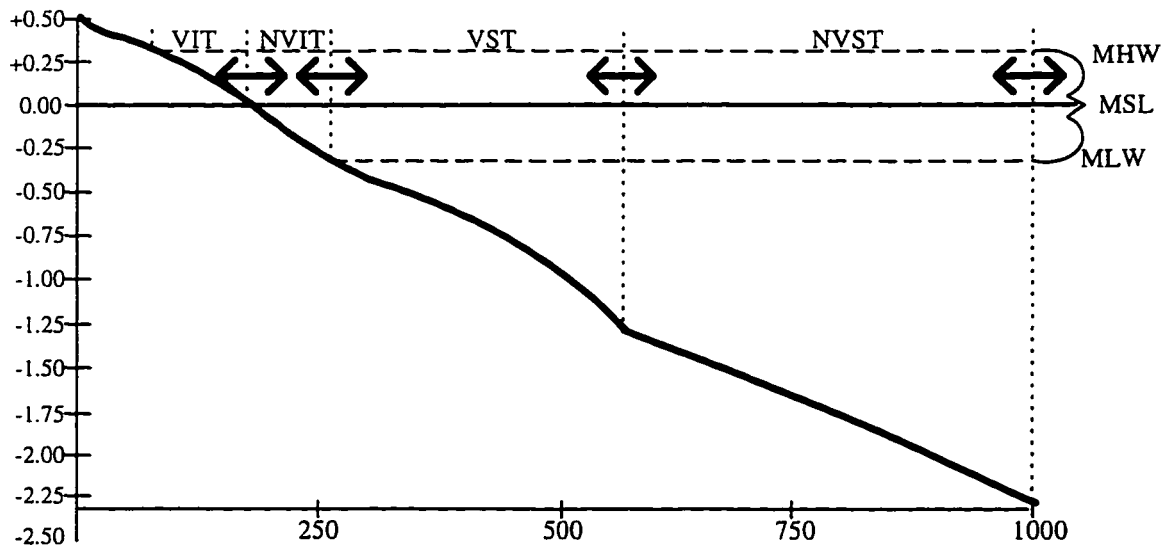
In May 1993, August 1993, and early December 1995 four cores (5.6 cm ID X

Figure 3. A generalized habitat map for the Goodwin Islands NERR. The four habitats were delineated according to elevation and biotic characteristics.

(A) Habitat Map for the Goodwin Islands Littoral Zone



(B) Goodwin Islands shoreface profile depicting distribution of littoral zone habitats



10.0 cm) were selected by hand from each of the sandy offshore (NVST), seagrass meadow edge (VST A), seagrass mid-meadow (VST B), and nonvegetated nearshore (NVIT) habitats for the determination of general sediment characteristics. The cores were stored on ice and transported to the laboratory. The overlying water was removed by siphon, the sediment was extruded, and cut into 0-2, 2-5, 5-10 cm sections. Subsamples of the sediment sections of one core were dried at 60° C for at least 96 hrs, finely ground, and preserved for the determination of total carbon and nitrogen contents using a Control Equipment Organization model 440 elemental analyzer (Dr. R.R. Christian, East Carolina University). Each section of the other three cores was weighed wet to determine bulk density (g wet cm^{-3}) and then split in half. One half was weighed wet, dried at 60° C for at least 96 hrs and re-weighed, and then combusted and re-weighed again to calculate water and organic contents (%H₂O and %OM, respectively). The other half-section was placed into a Whirlpak[®] with 100 ml of 2.0 N KCl for at least 30 minutes to extract the exchangeable inorganic nutrients. The extract was poured into a centrifuge tube and spun on a table top centrifuge at 3000 RPM for 10 minutes. The supernatant was decanted over Gelman GF/F filters (Type A/E, P/N 61631) to remove any remaining particulate matter and the filtered extracts were analyzed for total exchangeable NH_4^+ (μM) using the phenolhypochlorite technique (Greenberg et al., 1992) and total exchangeable $\text{NO}_3^- + \text{NO}_2^-$ (NO_x^- ; μM) using an Alpkem AutoAnalyzer.

Water Column Variables

Temperature, salinity, and chlorophyll *a* concentration are part of a series of water column variables that is determined along a salinity gradient in shoal environments of the York River, Virginia bi-weekly since 1984 (Batuik et al., 1992). In April 1993 the

Goodwin Islands shoal was added as a polyhaline station at the York River mouth. Water temperature, salinity, three 1.0 L bottles, and three 250 ml bottles of water were collected every two weeks at the Goodwin Island site between 28 April 1993 and 5 February 1996. Water temperature and salinity were determined using a YSI Model 33 meter. The samples were stored on ice for transport to the laboratory. In the laboratory the three 1.0 L samples were filtered over precombusted GF/F filters using a vacuum pump. The filters were dried at 60 ° C, weighed, combusted at 500 ° C, and re-weighed to determine ash free dry weight. Five ml of each of the 250 ml water samples were filtered through 25 mm Whatman GF/F filters using a vacuum pump. The filters were placed into opaque screw top test tubes with 8 ml of a 4.5:4.5:1 solution of dimethylsulfoxide (DMSO), acetone, and deionized water with 0.1% of diethylamine (DEA) for at least 24 hrs to extract the photopigments following the method of Shoaf and Lium (1976) as modified by Hayward and Webb (unpubl. data). The concentrations of chlorophyll *a* and phaeopigments ($\mu\text{g pigment L}^{-1}$) were calculated from fluorescence values before and after acidification with 2.0 N HCl using a Turner Designs Model 10-AU fluorometer. The average monthly chlorophyll *a* concentrations were calculated from all of the samples collected between 1993 and February 1996.

Sediment Microalgal Chlorophyll *a*

Small cores for the determination (2.4 cm X 1.0 cm) of sediment microalgal biomass (chlorophyll *a*) were collected from all four habitats in May 1994, August 1994, November 1994, and February 1995 following the stratified randomized design. Sample size for each habitat was determined using a component score calculated from habitat relative size and complexity. Five cores were taken from each of the two subtidal habitats (NVST and VST), seven cores were collected from the nonvegetated intertidal habitat (NVIT), and ten cores were collected from the vegetated intertidal marsh (VIT). The cores

were stored on ice for transport to the laboratory. In the laboratory the overlying water was removed carefully by siphon, the cores were extruded, and cut into 0-2, 2-5, and 5-10 mm sections using a microsectioning device. Each section was placed into a scintillation vial, frozen overnight, and then extracted with 10 ml of a 4.5:4.5:1 solution of methanol:acetone: water for three days (Pinckney et al., 1994). The vials were kept in a dark freezer and shaken daily for three days. The extracts were filtered using Gelman 0.45 μm Acrodisc CR PTFE filters and the concentration of chlorophyll a and total phaeopigments were calculated for the filtered extracts by measuring the absorbances at 750 and 665 nm before and after acidification with 10% HCl (Lorenzen, 1967).

Subtidal Vegetation

Seagrass biomass was determined monthly from May 1993 through April 1994 and the spatial characteristics of subtidal vegetation over the depth range were determined seasonally in a related study at the Goodwin Islands NERR (Moore et al., 1994). At monthly intervals five samples were collected randomly from within the seagrass meadow. Each sample consisted of the total plant biomass within a 0.1 m² ring placed on the sediment surface (Moore et al., 1994). The samples were dug from within the ring, rinsed across a 1.0 cm sieve to remove excess sediments, and stored on ice for transport to the laboratory. In the laboratory each sample was sorted by plant species (*Zostera marina* or *Ruppia maritima*) and each plant was rinsed of remaining sediment and counted. Shoot lengths were measured, the epiphytes were cleared, and the plants were separated into shoot and root-rhizome components. Biomass of the shoots and root-rhizomes were determined by weighing after drying at 60° C for at least 96 hrs.

In June 1993, August 1993, October 1993, and April 1994 a subtidal transect that spanned from the shoreline to the channel side of the seagrass meadow periphery was established to track seasonal spatial characteristics of the seagrass meadow (Moore et al.,

1994). At 10 m intervals along the transect relative depth, transect distance, sampling time, and percent vegetative cover were recorded. The relative depth was normalized to MLW using referenced tidal measurements at the National Ocean Survey tidal gauging station at Gloucester Point, VA, located approximately 10 km west in the York River (Moore et al., 1994). The depths were then corrected to reflect the MSL reference used in this study by assuming that $MSL = MLW + 0.36 \text{ m}$.

Subtidal Sediment-Water Exchanges

Vegetated and nonvegetated subtidal cores (11.6 cm X 15 cm) were collected from the subtidal habitats for flux experiments in June 1993, August 1993, October 1993, and March 1994. These seasonal sediment-water oxygen and nutrient exchange (SONE) studies were conducted to quantify vertical fluxes and identify trophic status in each of the subtidal habitats. Three to five cores were selected from each of the seagrass meadow and the adjacent nonvegetated subtidal areas and transported to a flowing seawater bath of the outdoor mesocosms at the Virginia Institute of Marine Science (VIMS) in Gloucester Point, VA. The water overlying the sediment within a core was replaced with filtered, partially degassed (approximately $4 \text{ mg O}_2 \text{ L}^{-1}$) water from the field site. The cores were stirred using battery powered submersible motors and were incubated for 4-6 daylight hours. Dissolved oxygen and inorganic nitrogen (NH_4^+ and NO_x^-) in the overlying water were sampled hourly. Oxygen was measured using an Orbisphere Oxygen probe while aqueous NH_4^+ and NO_x^- were analyzed using the colorimetric and autoanalytical methods similar to those described above for subtidal sediment inorganic nitrogen. Concentrations at each sampling time in $\mu\text{moles L}^{-1}$ were multiplied by overlying water volume to derive mass (μmoles) and then divided by core surface area (0.0105 m^2) to derive units of $\mu\text{moles m}^{-2}$.

The concentrations were then plotted over time using linear regression to determine the slope (or rate of change) in $\mu\text{moles m}^{-2} \text{hr}^{-1}$.

Intertidal Marsh Vegetation and Sediments

Within the vegetated intertidal marsh (VIT) a systematic randomized design was used to collect aboveground and belowground *Spartina alterniflora* biomass and sediment cores. Sampling locations were established at 25 meter increments along a 225 m transect that crossed low marsh (tall *Spartina alterniflora*), mudflat, salt panne, and high marsh (short *Spartina alterniflora*) habitats. GPS surveys in the intertidal marsh were conducted in June and August 1994 and at each sampling location the x, y, and z coordinates were determined using a Trimble GPS remote unit set to record satellite reference information at five second intervals for ten minutes. Clip plots of marsh vegetation and sediment cores were collected in September 1994, May 1995, and early December 1995 to capture summer, spring, and fall biomass signals. Three aboveground clip plots (0.1 m^2) were taken from each vegetated 25 m location that were randomized according to transect side (right or left) and distance normal to the transect (1, 2, or 3 meters). At locations representative of both the low and high marsh, two belowground cores (8.4 cm X 15.0 cm) were taken from each of the clip plot areas for a total of six sediment cores at each sampling location. Sediments were excavated to 15.0 cm depth because most of the live rhizome and root biomass is usually within this sediment layer (Gallagher and Howarth, 1987). Three of the six cores were used for the analysis of general sediment characteristics while the other three cores were used to determine belowground biomass. All of the cores and plants were placed into labelled plastic bags and stored on ice for transport to the laboratory.

In the laboratory each aboveground clip plot was sorted into live and dead fractions. The live shoots were counted and the five longest shoots were measured (cm) to determine

maximum shoot length. Some of the higher marsh clip plots included *Distichlis spicata* but only the data for the dominant marsh macrophyte, *Spartina alterniflora*, have been included. The live and dead aboveground fractions were placed into individually labelled paper bags, dried at 55° C for at least 96 hrs, and then weighed to determine dry weight biomass. Fractions of the dried shoots were finely ground for total C and N analyses. The three belowground biomass cores were broken up and rinsed repeatedly over a 1.0 mm sieve to remove all sediment. Due to difficulties associated with sorting salt marsh belowground live and dead biomass (see (Gross et al., 1991), all of the biomass contained in a core was included. The total belowground biomass of each core was placed into aluminum weighing pans, dried at 55° C for at least 96 hrs, and then weighed. A fraction of the dried belowground material was divided into roots and rhizomes and finely ground for total C and N analyses. The remaining sediment cores were used to determine general sediment characteristics and were processed similarly as described above for the subtidal and nearshore sediment cores except that they included an additional section (10-15 cm) and sub-samples for C and N analyses were pooled from the three cores rather than from an extra core.

Data Analysis

Each of the sediment variables (%OM, bulk density, %H₂O, NH₄⁺, and NO₃⁻) was averaged over the 3 (subtidal and nearshore) or 4 (intertidal marsh) sediment sections for each core collected. A two-way fixed effects ANOVA with season and habitat type as the independent variables was used to test the mean values of each sediment variable. The vegetated subtidal (VST) and intertidal (VIT) habitats were broken into two subhabitats to reflect meadow edge vs mid-meadow and low vs high marshes, respectively, bringing the total to six habitat types for the analysis of sediment variables. Since low marsh sediment

NH_4^+ was the only variable that exhibited seasonality the data for each variable in each habitat were pooled over the seasons. A one-way ANOVA with habitat type as the independent variable was then performed and Tukey's Honest Significant Difference (HSD) test for unequal sample sizes was used to differentiate the mean values of each sediment variable. The data on the concentrations of sediment microalgal chlorophyll *a* were treated similarly as for the other sediment variables (two-way fixed effects ANOVA) but only the four basic habitat types were included (NVST, VST, NVIT, VIT) and the data were not pooled over the seasons.

The spatial and temporal patterns of macrophyte growth characteristics (*Zostera marina* and *Spartina alterniflora*, respectively) were assessed using descriptive statistics. The average shoot density, shoot length, and shoot biomass were calculated for each sampling location of the intertidal marsh transect in order to analyze the spatial characteristics of marsh vegetation. A similar approach was adopted to analyze the spatial patterns of subtidal vegetation. Descriptive statistics were also used to analyze spatial patterns of sediment C:N over the gradient of elevation, the temporal patterns of water column variables, and the exchanges of oxygen and inorganic nitrogen between the sediment and overlying water in the subtidal habitats.

RESULTS

Sediment Biogeochemical Characteristics

Table 1 contains a summary of the sediment characteristics determined in this study. Sediment water content ($\%\text{H}_2\text{O}$) was lowest in the NVST habitat (20.73%) and greatest in the high marsh habitat (VIT H; 74.39%). Sediment water content was similar for the NVST, VST A, VST B, and NVIT habitats ($p > 0.05$) and differed significantly from the VIT L and VIT H habitats ($p < 0.01$). VIT L and VIT H also differed significantly from

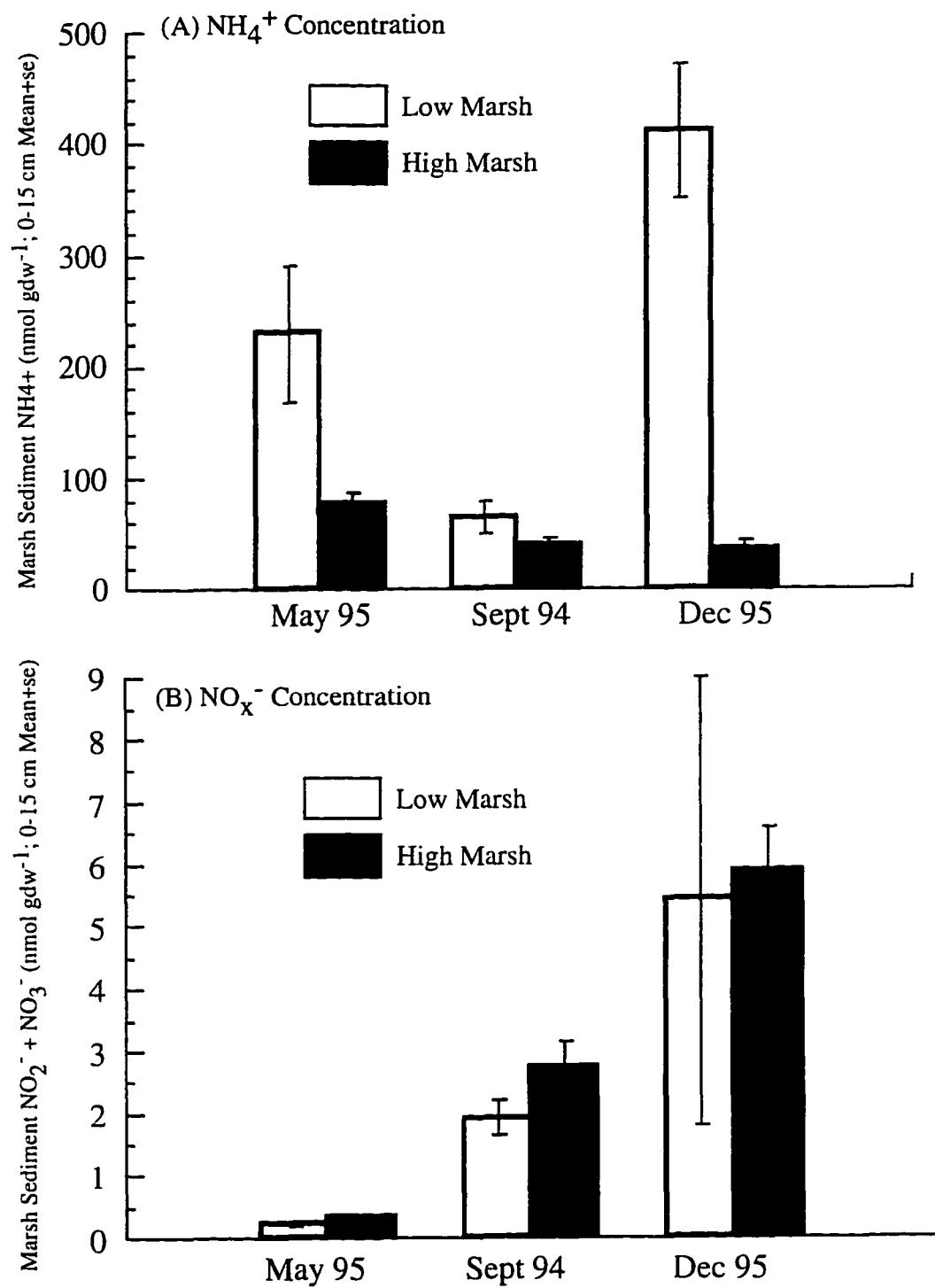
each other ($p < 0.01$). Sediment organic content (%OM) also was lowest in the NVST (0.57%) and highest in the VIT H (30.31%). Organic matter followed a similar pattern as water content where the NVST, VST A, VST B, and NVIT habitats were all similar ($p > 0.10$) but different from either the VIT L or VIT H habitats ($p < 0.01$). Sediment bulk density (g wet cm^{-3}) was similar for the NVST, VST A, VST B, and NVIT habitats ($p > 0.10$) but different from the two marsh habitats ($p < 0.01$), which were similar to each other ($p > 0.10$).

As previously mentioned the vegetated intertidal marsh did display some seasonality in the concentrations of exchangeable NH_4^+ and NO_x^- (nmol g dw^{-1} ; Fig. 4). The concentrations of NH_4^+ in the low marsh sediments were statistically different between the spring (May 1995) and fall (December 1995; Fig. 4A; $p < 0.01$). The NH_4^+ concentration did not vary seasonally for the high marsh sediments (Fig. 4A; $p > 0.05$). The concentration of NO_x^- in the high marsh sediments were statistically different between the summer (September 1994) and fall (December 1995; Fig. 4B; $p < 0.01$). The NO_x^- concentration did not vary seasonally for the low marsh sediments (Fig. 4B; $p > 0.05$). After pooling the seasonal data the nonvegetated subtidal habitat (NVST) had the lowest average sediment NH_4^+ concentration ($35.7 \text{ nmol g dw}^{-1}$) while the low intertidal marsh habitat (VIT L) was found to have the highest average concentration of exchangeable NH_4^+ ($403 \text{ nmol g dw}^{-1}$; Table 1). Exchangeable NH_4^+ concentrations were similar in the NVST, VST A, VST B, NVIT, and VIT H habitats ($p > 0.05$) and all of these habitats differed from the sediment of the VIT L habitat ($p < 0.05$; Table 1). Exchangeable NO_x^-

Table 1. Sediment characteristics for the Goodwin Islands NERR. The mean and standard error values for water content (% wet weight), organic matter (% dry weight), bulk density (gwt cm⁻³), and NH₄⁺ and NO_x⁻ concentrations (nmol gdw⁻¹) were averaged over sediment depth and season and are shown for each of the habitats including nonvegetated subtidal (NVST; n=9), vegetated subtidal meadow edge (VST A; n=9), vegetated subtidal meadow (VST B; n=9), nonvegetated intertidal (NVIT; n=9), low vegetated intertidal marsh (VIT L; n=10), and high vegetated intertidal marsh (VIT H; n=15). Superscripts denote statistical similarity among habitats for each of the sediment variables.

	Water Content (% H ₂ O)	Organic Matter (%OM)	Bulk Density (gwt cm ⁻³)	Exchangeable NH ₄ ⁺ (nmol gdw ⁻¹)	Exchangeable NO _x ⁻ (nmol gdw ⁻¹)
	mean±se	mean±se	mean±se	mean±se	mean±se
NVST	20.73±0.47 ^a	0.57±0.08 ^a	1.91±0.04 ^a	133.74±15.65 ^a	3.76±0.33 ^a
VST A	25.36±1.17 ^a	1.13±0.14 ^a	1.81±0.05 ^a	163.93±26.10 ^a	3.97±0.32 ^{ab}
VST B	22.82±1.15 ^a	0.80±0.13 ^a	1.83±0.08 ^a	161.88±23.05 ^a	2.72±0.41 ^a
NVIT	25.27±1.26 ^a	1.44±0.16 ^a	1.84±0.04 ^a	137.06±9.55 ^a	1.06±0.23 ^{ac}
VIT L	66.02±1.54 ^b	17.87±0.88 ^b	0.92±0.06 ^b	234.39±56.13 ^b	2.30±1.18 ^a
VIT H	74.39±0.81 ^c	30.31±0.92 ^c	0.99±0.03 ^b	54.39±6.87 ^a	2.41±0.58 ^a

Figure 4. NH_4^+ (Fig. 4A) and NO_x^- (Fig. 4B) concentrations (nmol gdw^{-1}) in the marsh sediment of the Goodwin Islands NERR. The 0-15 cm mean and standard errors are for low marsh and high marsh areas in May 1995, September 1994, and December 1995. The mean \pm standard errors are plotted.



(nmol gdw⁻¹) was lowest in the nonvegetated intertidal habitat (NVIT = 0.44) and highest in the high marsh sediments (VIT H = 14.1; Table 1). The average concentration of exchangeable NO_x⁻ (nmol gdw⁻¹) in the sediments of the NVST, VST A, VST B, and NVIT habitats were statistically similar ($p > 0.1$) but differed from both the VIT L and VIT H ($p < 0.05$ for both) habitats (Table 1).

Total carbon (gC gdw⁻¹) in the sediments was lowest in the seagrass meadow (VST B: 0.00083) and highest in the high marsh (VIT H: 0.19499; Table 2). Total nitrogen (gN gdw⁻¹) in the sediments was lowest in the NVST habitat (0.00020) and highest in the VIT H (0.01016). Sediment C:N weight ratios (gC gN⁻¹) were lowest at the offshore edge of the seagrass meadow (VST A: 3.00) and highest in the high marsh (VIT H: 19.2). The sediment C:N ratios provided in Table 2 reflect an offshore to marsh gradient that parallels the gradient of relative elevation along which the habitat boundaries were established.

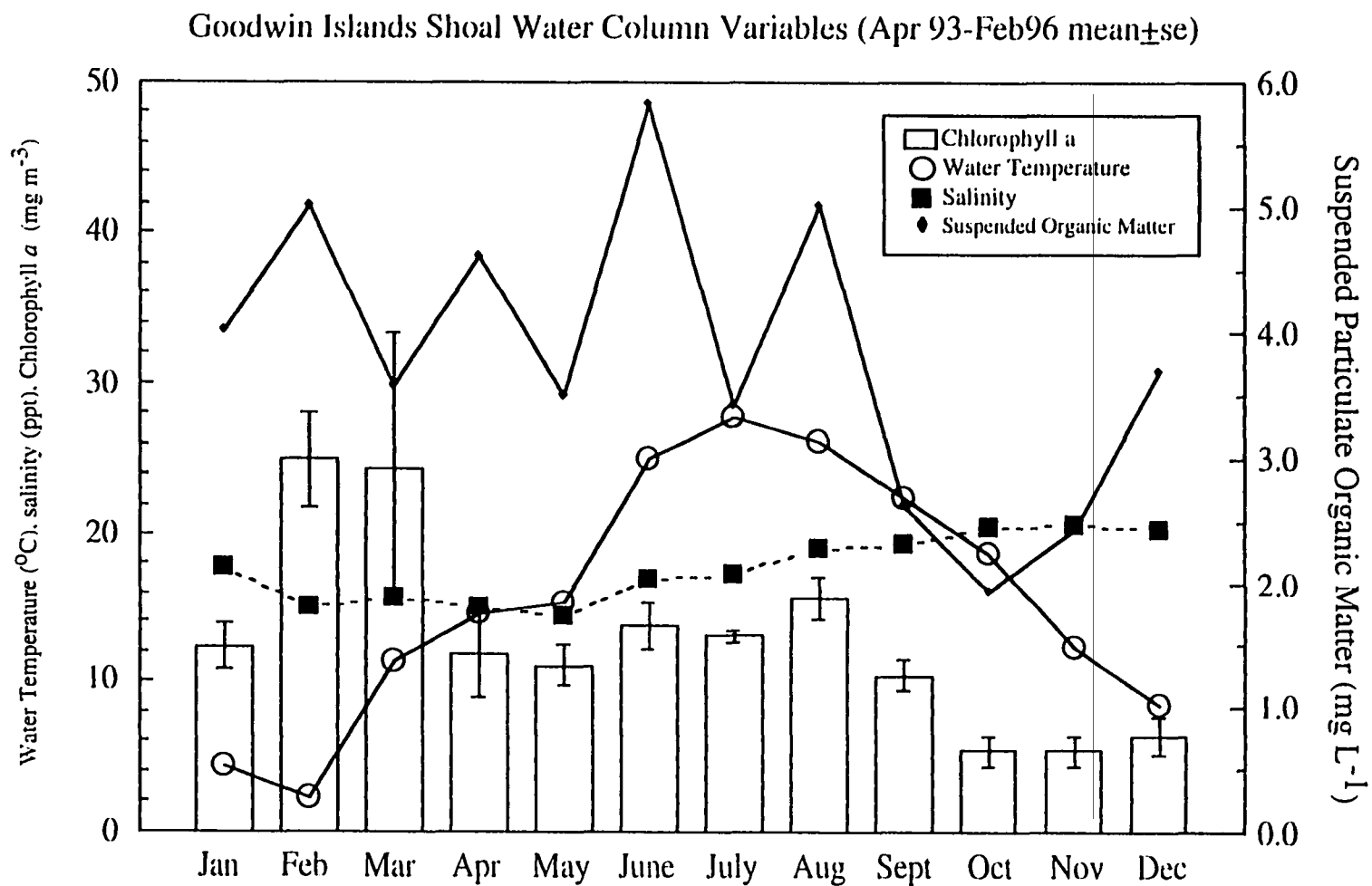
Water Column Variables

Average monthly water temperature at the Goodwin Islands was greatest in July at 29 °C and lowest in February at 2 °C (Fig. 5, open circles). Average monthly salinity did not change considerably between the minimum in May (14.5 ppt) and the maximum in October and November (20.9 ppt; Fig. 5, solid boxes). Average suspended particulate organic concentration (mgC L⁻¹) showed bimonthly maxima between January and August with the highest value of 5.8 mgC L⁻¹ in June followed by a low concentration in July (3.5 mgC L⁻¹; Fig. 5). The fall months had the lowest overall concentrations with a minimum of 1.9 mgC L⁻¹ in October (Fig. 5). Water column chlorophyll *a* concentrations were greatest in February and March at approximately 25 mg Chl *a* m⁻³ (Fig. 5). March also

Table 2. Sediment and macrophyte C and N contents and ratios for the Goodwin Islands NERR. Total organic carbon (gC gdw⁻¹) and nitrogen (gN gdw⁻¹) contents were determined from finely ground dried sediment and plant tissue subsamples. *Zostera* RR includes both roots and rhizomes. *Zostera marina* data provided courtesy of K.A. Moore.

Sediment Type or Plant Part	Carbon (gC gdw ⁻¹)	Nitrogen (gN gdw ⁻¹)	C:N (gC gN ⁻¹)
NVST	0.00087	0.00020	4.35
VST A	0.00090	0.00030	3.00
VST B	0.00083	0.00023	3.61
NVIT	0.00440	0.00047	9.36
VIT L	0.10417	0.00604	17.3
VIT H	0.19499	0.01016	19.2
<i>Zostera</i> Shoots	0.3553	0.0216	18.3
<i>Zostera</i> RR	0.3247	0.0131	26.2
<i>Spartina</i> Shoots	0.4099	0.0141	29.1
<i>Spartina</i> Roots	0.4167	0.0113	36.7
<i>Spartina</i> Rhizomes	0.3990	0.0070	56.8

Figure 5. Values for Goodwin Islands NERR shoal water column variables between April 1993 and February 1996 including the average monthly temperature ($^{\circ}\text{C}$), salinity (ppt), suspended organic matter (mgC L^{-1}), and the mean and standard error for water column chlorophyll *a* concentration ($\text{mg Chl } a \text{ m}^{-3}$).



had the greatest variability with a standard error of $8.98 \text{ mg Chl } a \text{ m}^{-3}$. The lowest average concentrations were in October-December at $5.3\text{-}6.4 \text{ mg Chl } a \text{ m}^{-3}$ (Fig. 5). All other months averaged $10.4\text{-}15.7 \text{ mg Chl } a \text{ m}^{-3}$.

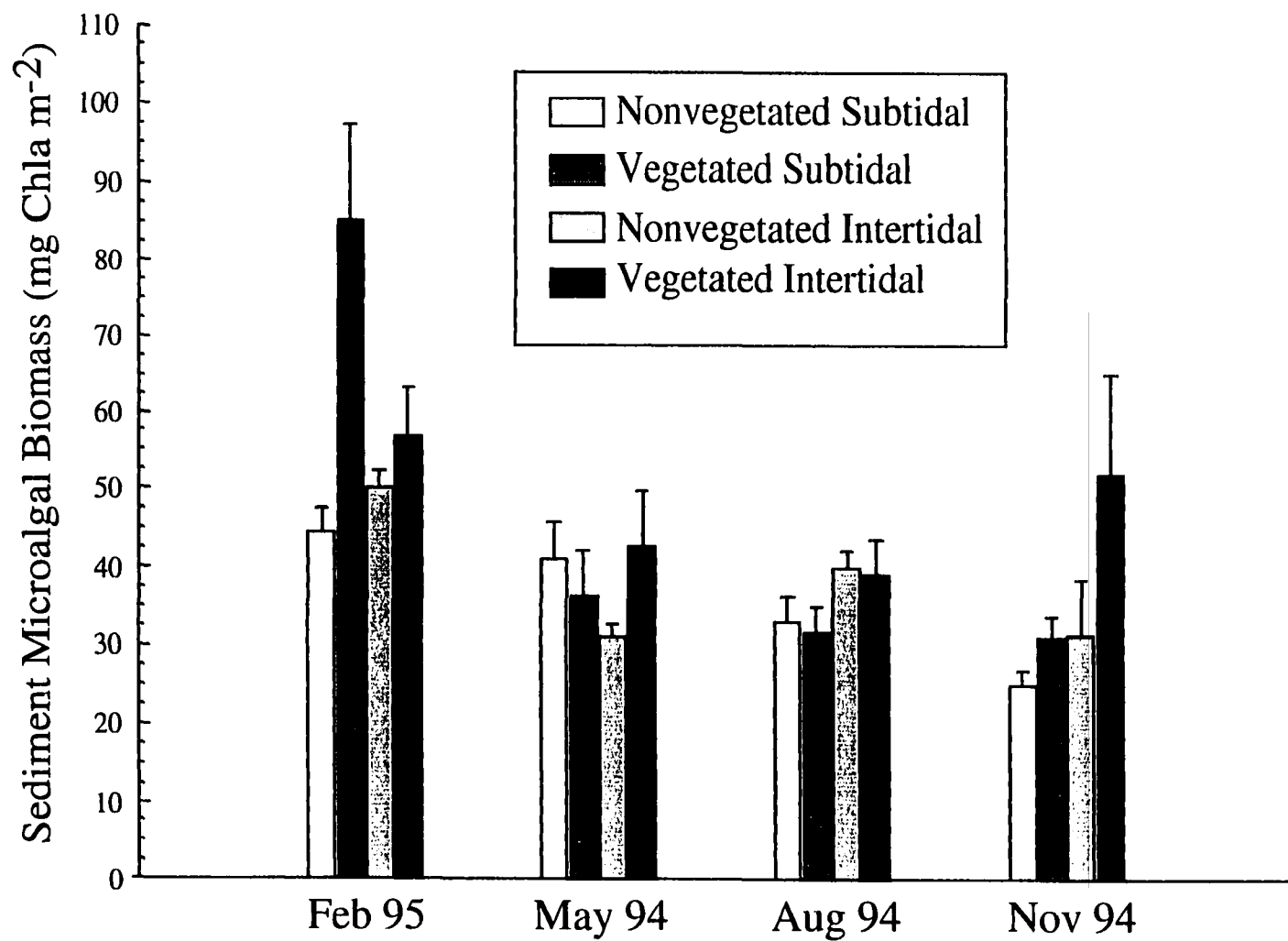
Sediment Microalgal Chlorophyll a

Sediment microalgal biomass is often measured by extracting chlorophyll a from the surface sediment and is considered to be directly correlated with rates of primary production (Pinckney and Zingmark, 1993). The 1.0 cm average and standard error values for the nonvegetated and vegetated subtidal (NVST and VST) and intertidal (NVIT and VIT) habitats are contained in Figure 6. The average sediment chlorophyll a concentration in the VST habitat in February ($85.3 \text{ mg Chl } a \text{ m}^{-2}$) was the highest recorded in any season or habitat while the NVST habitat had the lowest in November ($24.9 \text{ mg Chl } a \text{ m}^{-2}$). The VST was the only habitat that displayed significantly different seasonal values ($p < 0.05$) with the maximum in February and a minimum near $31.0 \text{ mg Chl } a \text{ m}^{-2}$ in August and November. In addition to there being no seasonality in the sediment chlorophyll a data for the NVST, NVIT, and VIT habitats there also were no statistical differences among the four habitats within each season ($p > 0.07$; Fig. 6). The grand mean and standard error for all cores collected between May 1994 and February 1995 were $42.9 \pm 2.45 \text{ mg Chl } a \text{ m}^{-2}$.

Subtidal Vegetation Characteristics

Buzzelli (1991) contains monthly C and N contents for *Zostera marina* shoot and root-rhizomes collected from a seagrass meadow located across the York River from the Goodwin Islands. In this study, *Zostera marina* shoot carbon averaged $0.3553 \text{ gC gdw}^{-1}$

Figure 6. Sediment microalgal biomass (mg Chl a m⁻²) for the nonvegetated and vegetated subtidal and intertidal habitats of the Goodwin Islands NERR in February 1995, May 1994, August 1994, and November 1994. The mean \pm standard errors are plotted.



while the roots + rhizomes (RR) averaged $0.3247 \text{ gC gdw}^{-1}$ seasonally (Table 2). Shoot nitrogen averaged $0.0216 \text{ gN gdw}^{-1}$ to provide a C:N of 18.3 (gC gN^{-1}) and the RR had $0.0131 \text{ gN gdw}^{-1}$ a C:N of 26.2 (Table 2). The results of the monthly *Zostera marina* biomass survey and the percent vegetative cover by over the depth gradient for June at the Goodwin Islands NERR from 1993-1994 are provided in Moore et al. (1994). *Zostera marina* shoot biomass (gdw m^{-2}) was greatest in June at 230.0 gdw m^{-2} and lowest in February and August at approximately 34 gdw m^{-2} . The root-rhizome biomass was greatest in May at 131.0 gdw m^{-2} and lowest in August at 21.5 gdw m^{-2} . The overall seasonal pattern of *Zostera marina* biomass is consistent with other research done in lower Chesapeake Bay (Orth and Moore, 1986). Depth ranged between -0.8 m and -1.2 m below MSL over a 550 m horizontal distance between the shoreline and the seagrass meadow periphery in June 1993. The vegetation was generally most dense in the middle portion of the transect between 150 and 300 m offshore and covered approximately 95% of the subtidal bottom at the 200 m distance. It is important to note that the spatial distribution and density of seagrass varies with the seasonal changes in biomass (Moore et al., 1994).

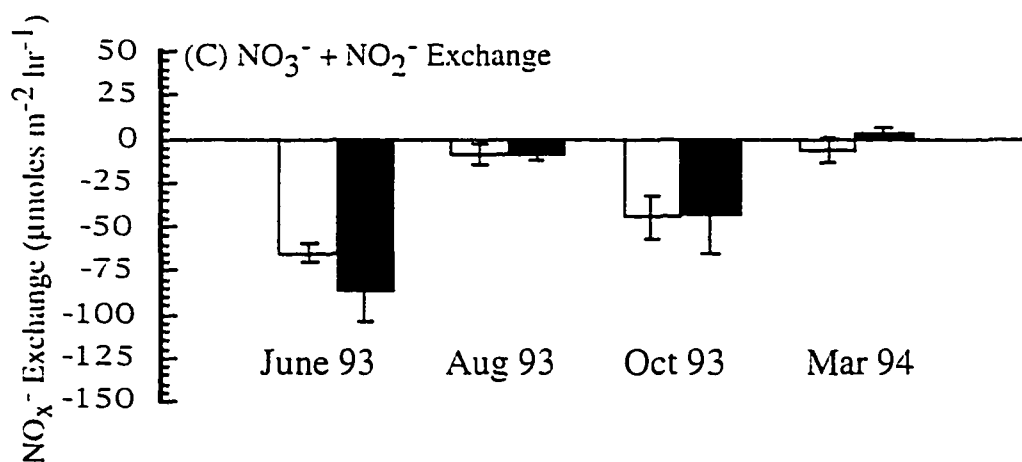
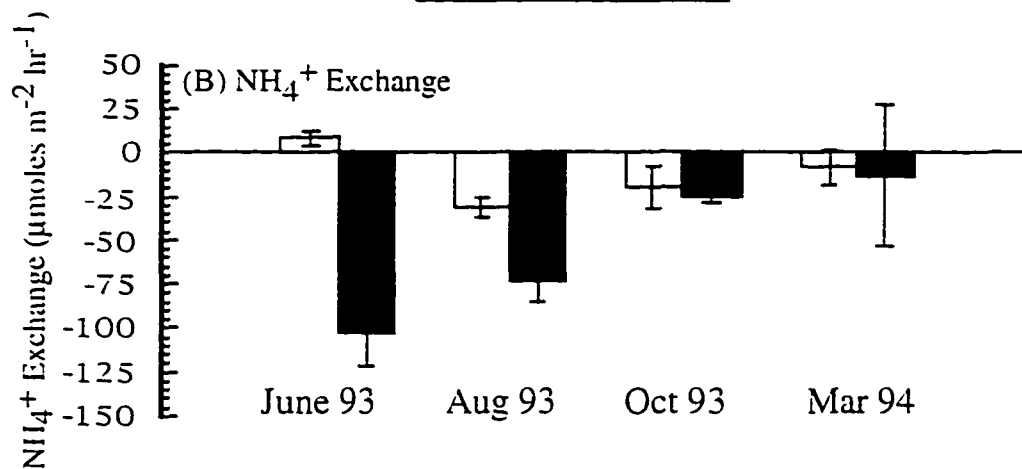
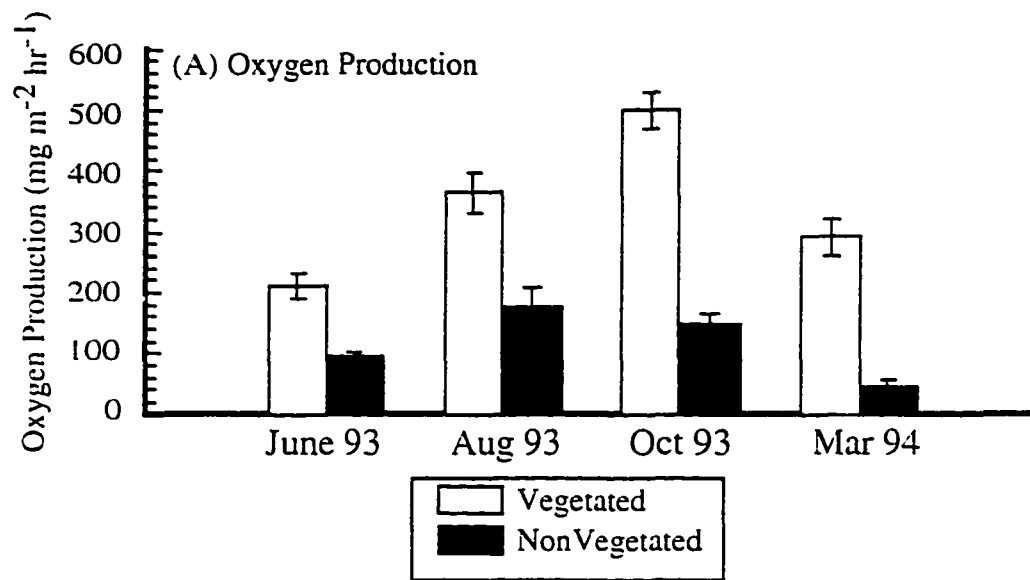
Sediment-Water Oxygen and Nitrogen Exchanges (SONE)

Vegetated and nonvegetated cores selected from the subtidal habitats (NVST and VST) were incubated under conditions representative of ambient temperature and irradiance in order to assess subtidal community trophic status (Fig. 7). No dark cores were incubated so the data reflect mid-day subtidal community autotrophic processes. A negative flux denotes uptake by the sediment community. Both vegetated and nonvegetated sediments provided a source of dissolved oxygen to the overlying water column in June 1993, August 1993, October 1993, and March 1994 (Fig. 7A). Average oxygen flux was

greatest in vegetated cores in October 1993 ($498 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$) and lowest in June 1993 ($210 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$). Nonvegetated oxygen production was 15-50% of that determined from vegetated cores in each of the seasonal experiments (Fig. 7A). Nonvegetated oxygen flux was greatest in August 1993 ($176 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$) and was lowest in March 1994 ($45 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$).

NH_4^+ and NO_x^- showed either minimal exchange or uptake by the sediment community for all seasons in each habitat type except for minimal positive fluxes to the overlying water in the vegetated cores in June 1993 and nonvegetated cores in March 1994 (Fig. 7B and 7C). Overall, seasonal NH_4^+ and NO_x^- exchanges were within similar ranges for both sediment types. Uptake of NH_4^+ by the vegetated sediment community was greatest in August 1993 ($-73 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$) and lowest in March 1994 ($-8.13 \pm 9.89 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$). There was a small release of NH_4^+ from the sediment to the overlying water recorded in June 1993 ($8.1 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$; Fig. 8B). Uptake of NH_4^+ by the nonvegetated sediment community was greatest in June 1993 ($-103 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$) and lowest in March ($-13.4 \pm 40.8 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$; Fig. 7B). Uptake of NO_x^- by the vegetated sediment community was greatest in June 1993 ($-65 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$) and lowest in August 1993 and March 1994 around $-7.5 \text{ } \mu\text{moles N m}^{-2} \text{ hr}^{-1}$ (Fig. 7C). Uptake of NO_x^- by the nonvegetated sediment community was greatest in June 1993 ($-87 \text{ } \mu\text{moles}$

Figure 7. Rates of sediment-water oxygen ($\text{mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$; Fig 7A), NH_4^+ ($\mu\text{moles m}^{-2} \text{ hr}^{-1}$; Fig. 7B) and, NO_x^- ($\mu\text{moles m}^{-2} \text{ hr}^{-1}$; Fig. 7C) exchange for the vegetated and nonvegetated sediments of the Goodwin Islands NERR in June 1993, August 1993, October 1993, and March 1994 derived using incubated cores. The mean \pm standard errors are plotted.



$\text{N m}^{-2} \text{ hr}^{-1}$) and lowest in August 1993 ($-8.6 \mu\text{moles N m}^{-2} \text{ hr}^{-1}$; Fig. 7C). There was zero flux of NO_x^- from the sediments in March 1994 ($3.31 \pm 3.35 \mu\text{moles N m}^{-2} \text{ hr}^{-1}$; Fig. 7C).

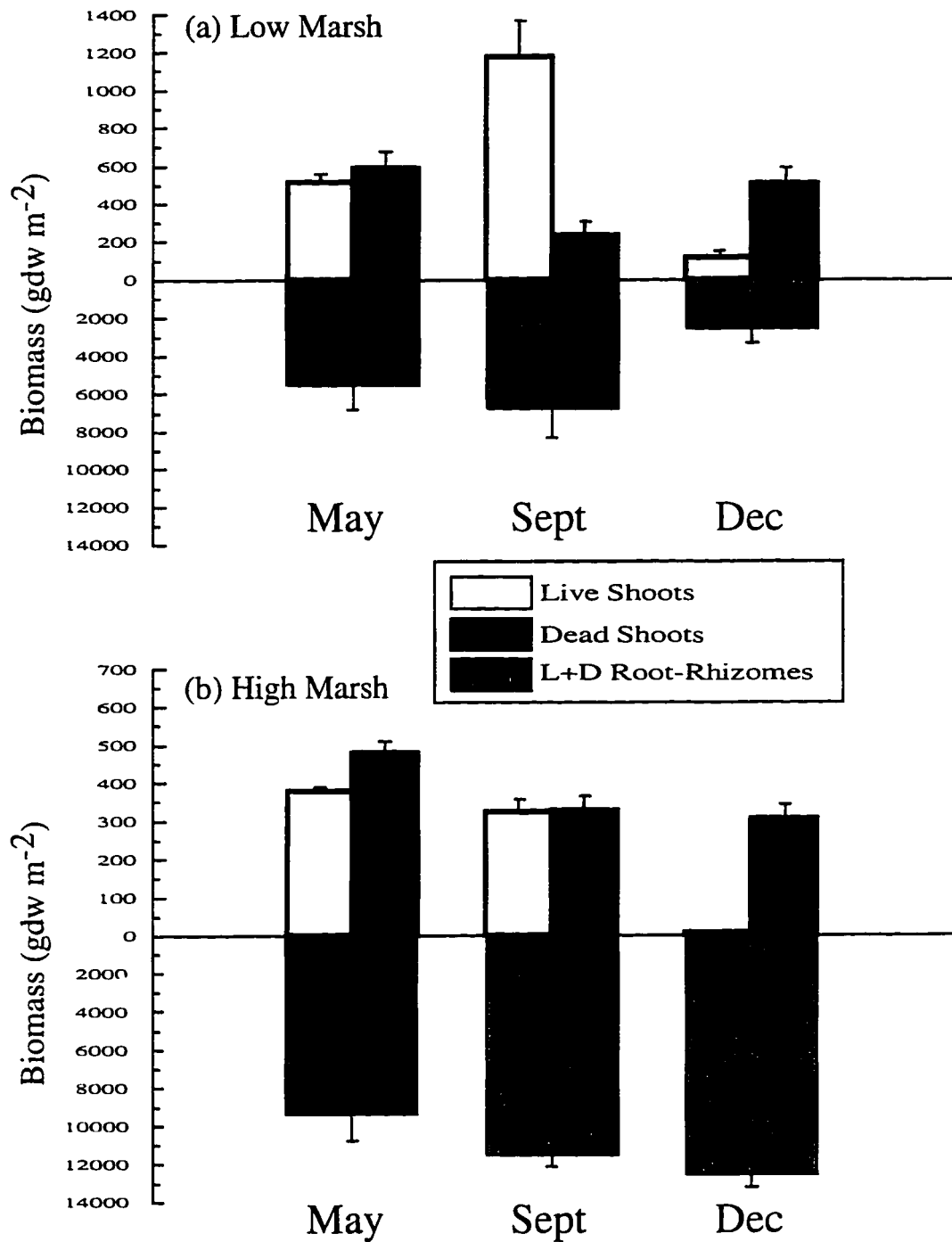
Intertidal Vegetation Characteristics

The C:N ratio of the shoots, roots, and rhizomes of *Spartina alterniflora* were 29.1, 36.7, and 56.8, respectively (Table 2). Since carbon content of each of these tissues was similar (around 0.4 gC gdw^{-1}), the variability in C:N reflects the decreased nitrogen content of each of the tissues ($0.014, 0.011, 0.007 \text{ gN gdw}^{-1}$). There was approximately four times more carbon in the tissues of *Spartina alterniflora* than in the sediments of the low marsh (0.4 vs 0.1 gC gdw^{-1}). There was approximately two times more organic nitrogen in the shoots and roots of *Spartina alterniflora* as in the low marsh sediments ($0.006 \text{ gN gdw}^{-1}$) while the nitrogen content of the rhizomes was similar to that of the sediments (Table 2).

Figure 8 summarizes the seasonal above and belowground biomass (gdw m^{-2}) of *Spartina alterniflora* of the Goodwin Islands marshes. The data were separated into low (Fig. 8A) and high marsh areas (Fig. 8B) to illustrate the differences in biomass among the two marsh elevations. Low marsh live (512 gdw m^{-2}) and dead (586 gdw m^{-2}) shoot biomass were similar in May 1995 but live shoot biomass climbed to 1176 gdw m^{-2} in summer and dead biomass dropped to 233 gdw m^{-2} (Fig. 8A). In early December 1995 there were only 115 gdw m^{-2} of live shoots present and about 500 gdw m^{-2} of dead *Spartina alterniflora* shoots remaining. High marsh live and dead shoot biomass were similar in May 1995 (377 vs 477 gdw m^{-2}) and September 1994 (321 vs 326 gdw m^{-2}) but

Figure 8. Shoot and root-rhizome biomass (gdw m⁻²) of *Spartina alterniflora* from the Goodwin Islands NERR. Live shoot, dead shoot, and total root-rhizome biomass were determined for low (Fig. 8A) and high marsh (Fig. 8B) areas in May 1995, September 1994, and, December 1995. Total root-rhizome biomass was all that was found within the top 15 cm of the sediment. The mean \pm standard errors are plotted.

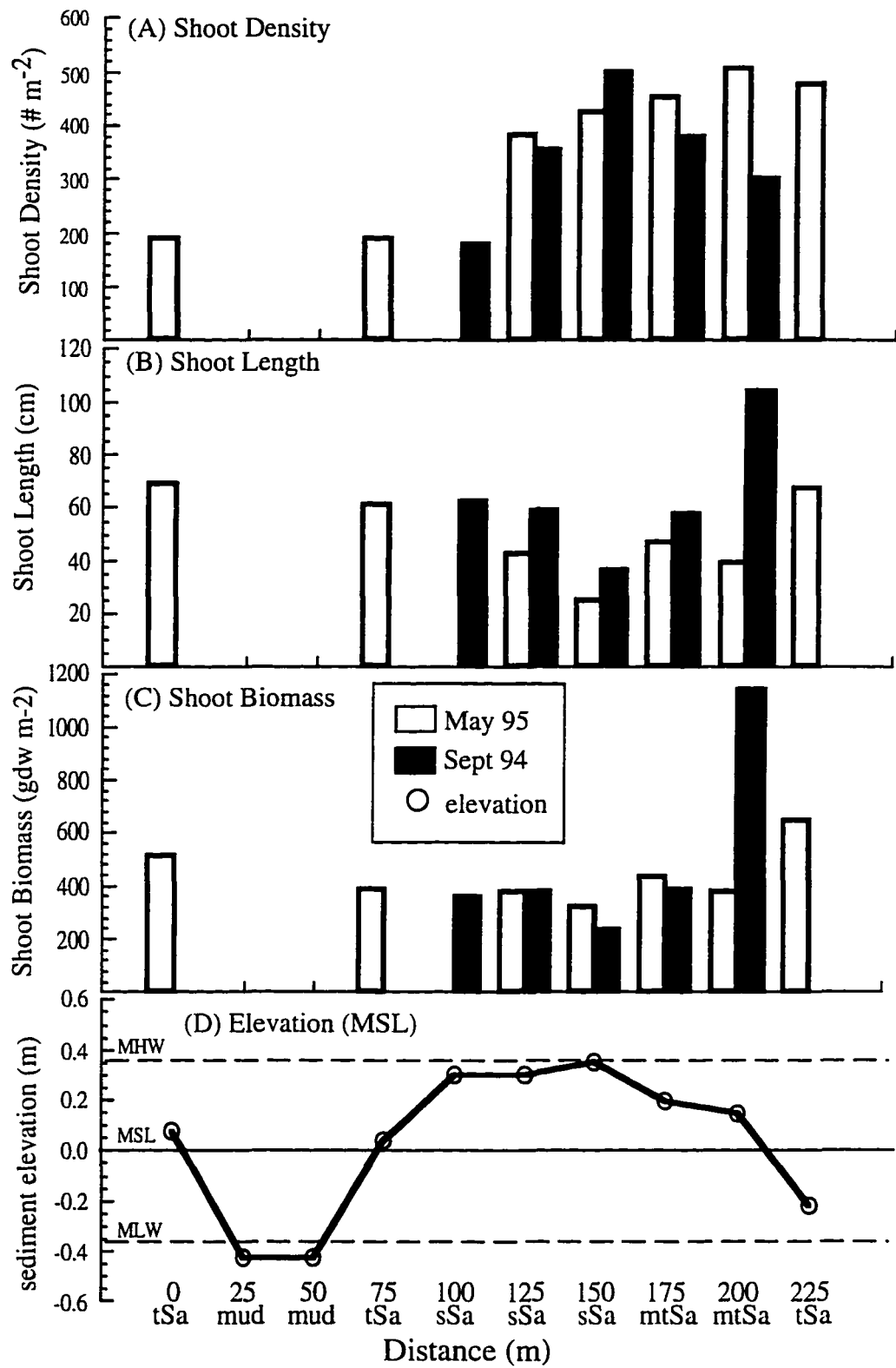
Goodwin Islands *Spartina alterniflora* Biomass



very little live shoot biomass remained in December 1995 (Fig. 8B). Although there were comparable amounts of live shoot biomass in the low and high marshes in May 1995 (512 vs 377 gdw m⁻²), by September 1994 there was approximately four times as much live shoot biomass in the low marsh (Fig. 8). Total belowground (live and dead roots and rhizomes) biomass in the low marsh averaged 5528, 6763, and 2547 gdw m⁻² in May 1995, September 1994, and December 1995, respectively (Fig. 8A) while total belowground biomass in the high marsh averaged 9381, 11526 and 12549 gdw m⁻² (Fig. 8B). The low marsh belowground biomass displayed some seasonality but the high marsh belowground biomass did not.

Figure 9A-D shows the shoot density, length, and biomass of *Spartina alterniflora* over the intertidal marsh transect in May 1995 and September 1994. Sediment elevation was determined from the GPS data at each sampling site over the sequence of low marsh, mudflat, and high marsh areas (Fig. 9D). Mean sea level and the mean high and low tidal water levels for Gloucester Point, Virginia were superimposed to show the distribution of marsh sediment elevation relative to tidal range. The low marsh grows near mean sea level, the mudflat sites are slightly below mean low water, and the high marsh extends to the mean high water level (Fig. 9D). Shoot density generally increased with sediment elevation in May 1995 although shoot density was greater at the 200 and 225 m locations than the higher marsh locations at 125 and 150 m (Fig. 9A). In September 1994 shoot density increased with elevation to a maximum of approximately 500 shoots m⁻² at the 150 m location which was 0.4 m above MSL. In May 1995 and September 1994 *Spartina alterniflora* shoot length displayed an inverse correlation with sediment elevation (Fig. 9B). In May 1995, shoots at low marsh locations 0 m and 225 m were approximately 70.0 cm in length while shoots at the highest marsh location (150 m) were only about 25.0 cm in length (Fig. 9B). In September 1994 shoots at the 200 m location averaged over 100 cm in

Figure 9. Shoot characteristics of *Spartina alterniflora* from the Goodwin Islands NERR in May 1995 and September 1994. The characteristics of shoot density (# m⁻²; Fig. 9A), shoot length (cm; Fig. 9B), and shoot biomass (gdw m⁻²; Fig. 9C) over the elevation range of the marsh (m; Fig. 9D).



length while shoots in the interior marsh at the 150 m location were only approximately 35.0 cm long. *Spartina alterniflora* shoot biomass in May 1995 at the low marsh ends of the transect (0 and 225 m) was 500-600 gdw m⁻² and shoot biomass between these two areas ranged from 300-450 gdw m⁻² (Fig. 9C). Shoot biomass was greatest at the 200 m location in September 1994 at approximately 1200 gdw m⁻² and biomass was similar or slightly less than that recorded in May 1995 at the interior marsh locations (Fig. 9C).

DISCUSSION

The Goodwin Islands NERR is similar to other littoral zone areas of lower Chesapeake Bay in that it contains sediment microalgal, seagrass, mudflat, and marsh habitats. To identify the pathways of material flux within the ecosystem and understand the potential exchange between the ecosystem and the boundary environments requires knowledge of the biogeochemical properties of the ecosystem components. This study provided the ecological background information essential to the development of ecosystem process models and established a ground truth data set for the generation of a geographic information system (GIS) for the Goodwin Islands NERR.

The sediment biogeochemical data show that the vegetated intertidal marsh habitat is quite different than either the offshore subtidal sediments or the nearshore nonvegetated intertidal sediments higher water and organic contents, lower bulk density, and higher concentrations of exchangeable NH_4^+ and NO_x^- (Table 1). The subtidal and nearshore sediments were remarkably consistent in sediment biogeochemical properties. The intertidal marsh sediments were more spatially and temporally heterogeneous in their properties than either the offshore or nearshore nonvegetated intertidal sediments. Seasonality in exchangeable DIN was evident only in the sediments of intertidal marsh as

NH_4^+ varied seasonally in the low marsh while NO_3^- varied seasonally in the high marsh (Fig. 4). The increased concentrations of NH_4^+ in the fall is assumed to result from decreased uptake of sediment NH_4^+ due to the decline of marsh plant productivity relative to normal or increased rates of nitrogen remineralization in the sediment rhizosphere.

The monthly average temperature, salinity, chlorophyll *a* concentrations, and suspended organic matter concentrations observed in the shoal water column provide insight into the seasonal relationships between phytoplankton and environmental factors. Increased chlorophyll concentration in the winter and early spring usually reflects increased riverine discharge (Mallin, 1994; Malone et al., 1988). This assertion is somewhat supported by the salinity and suspended matter data where enhanced freshwater discharge in the winter was represented by decreased salinity but not necessarily by increased suspended organic concentrations (Fig. 5). The hydrodynamic influence was more evident in the fall as chlorophyll *a* and suspended matter concentrations were minimal as salinity was greatest (Fig. 5). The overall concentrations of water column chlorophyll *a* found in this study (5-25 mg Chl *a* m^{-3}) were similar to those reported for the lower York River and the Neuse River in North Carolina (Batuik et al. 1992; Mallin, 1994).

With the exception of the seagrass meadow in February 1995, sediment microalgal biomass (mg Chl *a* m^{-2}) varied little spatially or seasonally (Fig. 6). Table 3 provides a comparison between the data reported here and other studies of sediment microalgal biomass in similar estuarine environments. The concentrations of sediment microalgal biomass reported for polyhaline, nonvegetated subtidal sediments of the Ems estuary (de Jonge and Colijn, 1994) averaged 62.2 mg Chl *a* m^{-2} (Table 3) while the South Carolina sandflat studied by Pinckney and Zingmark (1993) averaged 75.2 mg Chl *a* m^{-2} annually.

These values are almost twice the average determined for the NVST of the Goodwin Islands NERR (35.9). The average and standard error for microalgal biomass in the sediments of seagrass meadow in the Gulf of Mexico (Daehnick et al., 1992) were 43.6 ± 5.52 mgChl a m^{-2} while those determined for the eelgrass meadow in this study were 46.1 ± 13.1 mgChl a m^{-2} (VST; Table 3). The Massachusetts mudflat studied by Gould and Gallagher (1990) had a very large range of microalgal biomass (75-278) and the average was significantly higher than the NVIT habitat of the Goodwin Islands NERR (158.5 vs 38.1; Table 3). The average biomass of the NVIT sediment was approximately half that of a mudflat habitat studied in North Inlet, South Carolina (Pinckney and Zingmark, 1993). The average microalgal biomass reported for marsh sediment in Mississippi (Sullivan and Moncreiff, 1988) ranged 5-47 mgChl a m^{-2} and averaged 14.3 mgChl a m^{-2} (Table 3). The average sediment microalgal biomass below short *Spartina alterniflora* was 74.3 mgChl a m^{-2} while that below tall *Spartina alterniflora* was 103.5 mgChl a m^{-2} in South Carolina (Pinckney and Zingmark, 1993). The biomass range (39-57) and average (47.8 mgChl a m^{-2}) determined in the vegetated intertidal marsh of the Goodwin Islands NERR were between the concentrations reported for the Mississippi and South Carolina marshes (Table 3).

Despite periodic fluctuations in the distribution and abundance of subtidal vegetation in the Goodwin Islands NERR, the seagrass meadows are historically stable and are the only remaining meadow on the south shoreline of the York River. Although there is some widgeongrass (*Ruppia maritima*) nearshore at the Goodwin Islands NERR, a majority of the vegetation is *Zostera marina* (Moore et al., 1994). *Zostera marina* shoot biomass recorded at the Goodwin Islands NERR was similar to the range of 60-336 gdw m^{-2} reported for other estuarine locations (Orth and Moore, 1986; Roman and Able,

Table 3. Data comparison for sediment microalgal biomass (mg Chl *a* m⁻²) among estuaries. Habitats include nonvegetated subtidal, seagrass meadow, intertidal mudflat, and *Spartina alterniflora* marsh. Studies were conducted in the Ems estuary, the Netherlands (deJong and Colijn 1994), the Gulf of Mexico (Daenick et al. 1992), Savin Hill Cove, Massachusetts (Gould and Gallagher 1990), Graveline Bay, Mississippi (Sullivan and Moncreiff 1988), North Inlet, South Carolina (Pinckney and Zingmark 1993), and the Goodwin Islands, Virginia (this study).

Location	Habitat	Range	Mean±se	Literature Source
Netherlands	Nonvegetated	20-175	62.2±6.48	deJong and Colijn
Mississippi	Seagrass	30-82	43.6±5.52	Daenick et al.
Massachusetts	Mudflat	75-278	158.5±14.2	Gould and Gallagher
Mississippi	<i>Spartina</i> Marsh	5-47	14.3±4.29	Sullivan and Moncreiff
South Carolina	Sandflat	45-115	75.2±6.98	Pinckney and Zingmark
	Mudflat	60-105	72.5±5.54	..
	Short <i>Spartina</i>	45-105	74.3±6.11	..
	Tall <i>Spartina</i>	65-160	103.5±10.6	..
Virginia	NVST	24-45	35.9±4.39	This Study
	VST	31-85	46.1±13.1	..
	NVIT	31-50	38.1±4.49	..
	VIT	39-57	47.8±4.03	..

1988; Thorne-Miller et al., 1983). Root-rhizome biomass was within the range of published biomass estimates (61-175; Kenworthy and Thayer, 1984; Orth and Moore, 1986). The average nitrogen content of the shoots and root-rhizomes of *Zostera marina* in this study (0.0216 and 0.0131 gN gdw⁻¹, respectively; Table 2) was approximately twice those reported in Murray et al. (0.012 and 0.006 gN gdw⁻¹; 1992). Although seagrasses historically survived to the -2.0 m depth (MLW), seagrass meadows currently extend to -1.0 m (MLW) because they are sensitive to long term changes in environmental factors such as submarine irradiance and inorganic nutrients (Dennison et al., 1993). A transition from vegetated to nonvegetated subtidal bottom not only means a loss of critical habitat but could signify a change in community metabolism and trophic status. The subtidal sediment-water oxygen and nutrient exchange studies (SONE) were conducted to address these issues and the simulation models of the NVST and VST habitats have been developed to test hypotheses concerning the potential effects seagrass loss has upon water quality processes in the littoral zone.

The results of the SONE studies show that although the eelgrass community produces considerably more oxygen per unit area than the nonvegetated subtidal community, the nonvegetated sediments can meet or exceed the dissolved inorganic nitrogen removal potential of the eelgrass sediments (Fig. 7A-C). The range of 200-500 mg O₂ m⁻² hr⁻¹ measured for the seagrass sediments of this study (Fig. 7A) was higher than the average hourly net community production determined at a polyhaline location in the Neuse River, North Carolina (73.9 mg O₂ m⁻² hr⁻¹; Rizzo et al., 1992). The eelgrass community maximum oxygen fluxes did compare favorably with those collected using in situ plexiglass domes at the Goodwin Islands NERR during the same time as the June SONE study (Seufzer, 1994). The nonvegetated community net oxygen flux varied from

50 to 200 mg O₂ m⁻² hr⁻¹ seasonally and was within range of published values of daytime shoal metabolism (Rizzo et al., 1992). Nonvegetated subtidal sediments removed more NH₄⁺ from the water column in June 1993 and August 1993 than the adjacent vegetated sediments (Fig. 7B) while NO_x⁻ removal rates were similar among vegetated and nonvegetated sediments in all seasons (Fig. 7C). These studies addressed daytime trophic status in the subtidal vegetated and nonvegetated communities and have been used to represent sediment-water exchanges in the simulation models of the NVST and VST habitats (Buzzelli Section C). Further SONE types of studies currently are being conducted at the Goodwin Islands NERR to include more cores per sediment type, to calculate the nonvegetated and vegetated exchange rates in the dark, to measure rates of sediment nitrogen mineralization and nitrification, and to link measurements of primary production made at fine scales of resolution (cores) with intensive field studies of water column processes conducted in 1993-94 (I.C. Anderson and K.A. Moore, Virginia Institute of Marine Science).

The low marsh experienced a summer maximum shoot biomass and displayed some seasonal variation in total belowground biomass (Fig. 8A). The high marsh areas displayed reduced seasonal variability in aboveground biomass and maintained consistent total belowground biomass over all three seasons (Fig. 8B). These data support the assertion that *Spartina alterniflora* at lower elevations (near the creekbank) produces significantly more shoot biomass than plants located at higher elevations (Gross et al., 1991). The spatial relationships between sediment elevation, shoot density, and shoot length for *Spartina alterniflora* across the Goodwin Islands NERR marsh transect also supported previous studies conducted on salt marsh zonation (Gross et al., 1991; McKee and Patrick, 1988). Taller plants with increased shoot biomass and decreased density

survive at lower elevations and these characteristics were evident during the biomass maximum in September 1994 (Fig. 9A, 9B, 9D).

Table 4 provides a comparative summary of the maximum biomass attained by the shoots and root-rhizomes of *Spartina alterniflora* among estuarine locations. Although definitions vary with geographic location and marsh hydroperiod, *Spartina alterniflora* from the low marsh of the Goodwin Islands NERR were categorized as “tall” while those from the high marsh were termed “short” for the purposes of this discussion. The maximum biomass of tall plants in Delaware (1349 gdw m⁻²; Gross et al., 1991) was similar to that determined for the Goodwin Islands NERR (1176 gdw m⁻²; Table 4). Tall plants attained a lower maximum biomass in Massachusetts (650 gdw m⁻²; Roman et al., 1990) while the average aboveground biomass of all shoot length classes of *Spartina alterniflora* studied in Georgia was 733 gdw m⁻² (Schubauer and Hopkinson, 1984). The range of values for short *Spartina alterniflora* shoot biomass was between 322 (this study) and 500 gdw m⁻² (Mendelssohn, 1973) with some consistency among estuarine locations (Table 4). The average maximum values of total belowground biomass for tall *Spartina alterniflora* were similar in Georgia (Schubauer and Hopkinson, 1984) and Delaware (Gross et al., 1991) at 4480 and 4012 gdw m⁻² (Table 4). These values were less than those estimated for the low marsh areas of the Goodwin Islands NERR (6763 gdw m⁻²). Estimates of belowground biomass vary greatly with 6838 gdw m⁻² reported for Delaware (Gross et al., 1991), 9400 gdw m⁻² reported for New Jersey (Smith et al., 1979), and 11526 gdw m⁻² estimated at the Goodwin Islands NERR (Table 4). Overall, the shoot and root-rhizome biomass of *Spartina alterniflora* found in low and high marsh areas are within range of published estimates for other estuarine marshes of the Atlantic coast.

Table 4. Data comparison for *Spartina alterniflora* maximum biomass (gdw m⁻²) among estuarine locations. Categories include live shoots and total root-rhizome biomasses for "tall" and "short" plant growth forms. Data were taken from studies in Georgia (Schubauer and Hopkinson 1984), Delaware (Gross et al. 1991), New Jersey (Smith et al. 1979), Massachusetts (Roman et al.1990), South Carolina (Morris and Haskin 1990), and Virginia (Mendelssohn 1973 and this study).

Location	Month	Shoots		Roots + Rhizomes		Lit. Source
		Tall	Short	Tall	Short	
Georgia	Sept/Oct	733 ^a		4480 ^b		Schub. and Hopk. 1984
Delaware	June-Sept	1349	356	4012	6838	Gross et al. 1991
New Jersey	June-July		477		9400	Smith et al. 1979
Massachusetts	July	650	400			Roman et al. 1990
South Carolina	September		463			Morris and Haskin 1990
Virginia	September		500			Mendelssohn 1973
Virginia	September	1176	322	6763	11526	This Study

^a Average for all shoot length classes measured

^b Average of five individual sample means.

This study was conducted in support of efforts to link field data collection, geographic information technology, and the dynamic simulation of key living resources in multiple habitats of the Chesapeake Bay littoral zone. Despite being the smallest among the four habitats analyzed in this study of the Goodwin Island NERR, the intertidal marsh is the most spatially heterogeneous. The marsh sediments differed significantly with those of the subtidal and nearshore habitats in terms of sediment carbon and nitrogen characteristics. While phytoplankton biomass displayed some seasonality related to riverine discharge, sediment microalgal biomass did not vary significantly spatially or temporally in this study. The abundance of vegetation in both subtidal (*Zostera marina*) and intertidal (*Spartina alterniflora*) habitats displayed seasonal patterns in coverage and biomass that were consistent with other Atlantic estuarine ecosystems. This study was an essential prelude to the development of a series of mathematical models designed to simulate water column primary production and nitrogen cycling in the four primary littoral zone habitats of the Goodwin Islands NERR. Habitat size, extent, and composition determined in this study were used to establish model habitat boundaries and initial conditions and the data collected on water column and sediment variables, sediment-water exchanges, and macrophyte carbon and nitrogen characteristics were used as calibration information during model development (Buzzelli Section 3).

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Section 3

DEVELOPMENT OF SIMULATION MODELS FOR LITTORAL ZONE HABITATS OF
THE GOODWIN ISLANDS NATIONAL ESTUARINE RESEARCH RESERVE IN
LOWER CHESAPEAKE BAY

*To be submitted to Ecological Modeling.

ABSTRACT

Process oriented modeling of ecosystem dynamics can be used to organize information, identify missing data, and investigate the structure, function, and potential change of ecosystems. Littoral zone ecosystems of lower Chesapeake Bay contain a mosaic of shallow subtidal sand, seagrass meadow, mudflat, and intertidal marsh habitats that are connected by the exchange of waterborne materials. This study developed a series of four process oriented models designed to simulate primary production and material flux in the littoral zone habitats of the Goodwin Islands National Estuarine Research Reserve in lower Chesapeake Bay. The models were designed to represent nonvegetated subtidal, vegetated subtidal, nonvegetated intertidal, and vegetated intertidal habitats. Each model has sediment microalgae and water column phytoplankton, particulate organic carbon, dissolved organic carbon, and dissolved inorganic nitrogen. In addition to these variables the two vegetated habitats contain *Zostera marina* and *Spartina alterniflora*, respectively. The models were developed and calibrated using local and literature information. Model output was validated using independent data sets collected at the Goodwin Islands NERR or assembled from the literature. The models were developed as research tools to assist in the investigation of ecosystem dynamics in the littoral zone of lower Chesapeake Bay.

INTRODUCTION

Littoral zone ecosystems historically have not been included in efforts to simulate environmental processes in Chesapeake Bay although approximately 40% of the subtidal area is ≤ 2.0 m below MLW (Spinner, 1969; Cerco, 1993; Kuo and Park, 1995). The littoral zone environments of the Chesapeake Bay exhibit patterns of aquatic productivity, sediment processes, and biogeochemical cycling that are distinct from those of adjacent channel environments (Malone et al., 1986; Kuo and Park, 1995). Few published studies have utilized mechanistic models to analyze habitat interactions among coastal ecosystem components in order to identify the probable linkages to other areas of the landscape (Costanza et al., 1990; Boumans and Sklar, 1990; Childers et al., 1993). It is important to provide mechanistic models to help address issues related to environmental change in coastal environments (Costanza et al., 1990; Wetzel and Hopkins, 1990).

Understanding of the synergistic interactions among littoral zone habitats provides an essential link between the preservation of environmental quality and the protection of living resources such as macrophyte communities and fishery populations (Heck and Thoman, 1984; Dennison et al., 1993; Kneib and Wagner, 1994).

Estuarine landscapes are mosaics of subtidal and intertidal vegetated and nonvegetated habitats including shallow sandy shoals, seagrass meadows, mudflats, and low and high marshes (Correll et al., 1992). The estuarine flank environments exhibit bi-directional exchange of channel derived inorganic nutrients and shoal derived particulate materials (Malone et al., 1986; Kuo and Park, 1995). Depending upon the configuration of the landscape, the various littoral zone ecosystem components possess different biogeochemical connections that are regulated through meteorologic and hydrodynamic forces (Correll et al., 1992; Vorosmarty and Loder, 1994). In particular, ecosystems that contain irregularly inundated marshes can display periodicity in patterns of water chemistry and discharge to the adjacent habitats (Vorosmarty and Loder, 1994). The exchanges

(imports or exports) of inorganic or organic materials (dissolved or particulate) between marshes and the surrounding estuary depends upon the marsh developmental history and resulting basin configuration and hydroperiod (Childers et al., 1993).

Different approaches have been employed to mathematically represent stocks and processes in coastal ecosystems. Approaches include but are not limited to empirical modeling using regression (Dame et al., 1991) or other matrix methods (Keller, 1989; Dennison et al., 1993), network analysis (Baird and Ulanowicz, 1989), dynamic budgeting (Childers et al., 1993), mechanistic modeling of dynamic interactions (Wetzel and Hopkinson, 1990; Christian and Wetzel, 1991; Bach, 1993), and combinations (Morris, 1982; Morris et al., 1984). These various studies address specific aspects of individual primary producers in the littoral zone. None of the studies listed above have included suites of primary producers within a variety of hydrodynamically linked habitats. Simulation modeling provides the opportunity to organize information and initiate research and can be joined with geographic techniques to provide a framework in which to investigate dynamic coastal landscapes (Costanza et al., 1990; Christian and Wetzel, 1991; Lee et al., 1992; Childers et al., 1993).

The primary objective of this study was to develop a series of dynamic models to simulate water column processes and sediment primary production in the littoral zone habitats of the lower reaches of Chesapeake Bay. These models have been developed as research tools to organize available data, identify missing information, investigate the ecological linkages within the littoral zone, and generate new hypotheses to guide future research. The models are also used to investigate ecosystem structure, function and potential change (Buzzelli Section 4). Model background, mathematical structure, sensitivity to selected parameters, and validation results are presented and discussed in this summary.

METHODS

Study Site

The Goodwin Islands National Estuarine Research Reserve (NERR) is an 800 hectare (ha) littoral zone ecosystem at the mouth of York River in lower Chesapeake Bay (Buzzelli Section 2). The Goodwin Islands NERR is an oblong island system with a large subtidal shoal extending between the shoreline and the -2.0 m (MLW) depth contour (Fig. 1). Between -1.0 and -0.5 m (MLW) are approximately 120 hectares of subtidal seagrass meadows mostly comprised of eelgrass (*Zostera marina* L) (Fig. 1). There are approximately 100 hectares of nonvegetated intertidal habitats with fine sands and silty sediments that surround 85 hectares of intertidal marsh vegetated primarily by *Spartina alterniflora* although with higher regions vegetated by *Spartina patens* and *Distichlis spicata* and some small patches of *Juncus roemerianus*. The intertidal marsh grades into a saltbush community and finally into maritime forest and a small amount of upland. Coverage of vegetated subtidal and intertidal habitats vary over time (seasonally-interannually) and space (10's-100's ha). Historical aerial photography (1937-1990) depicts long term persistence and resilience in the Goodwin Islands NERR eelgrass meadows but overall erosion and some horizontal migration for intertidal marshes.

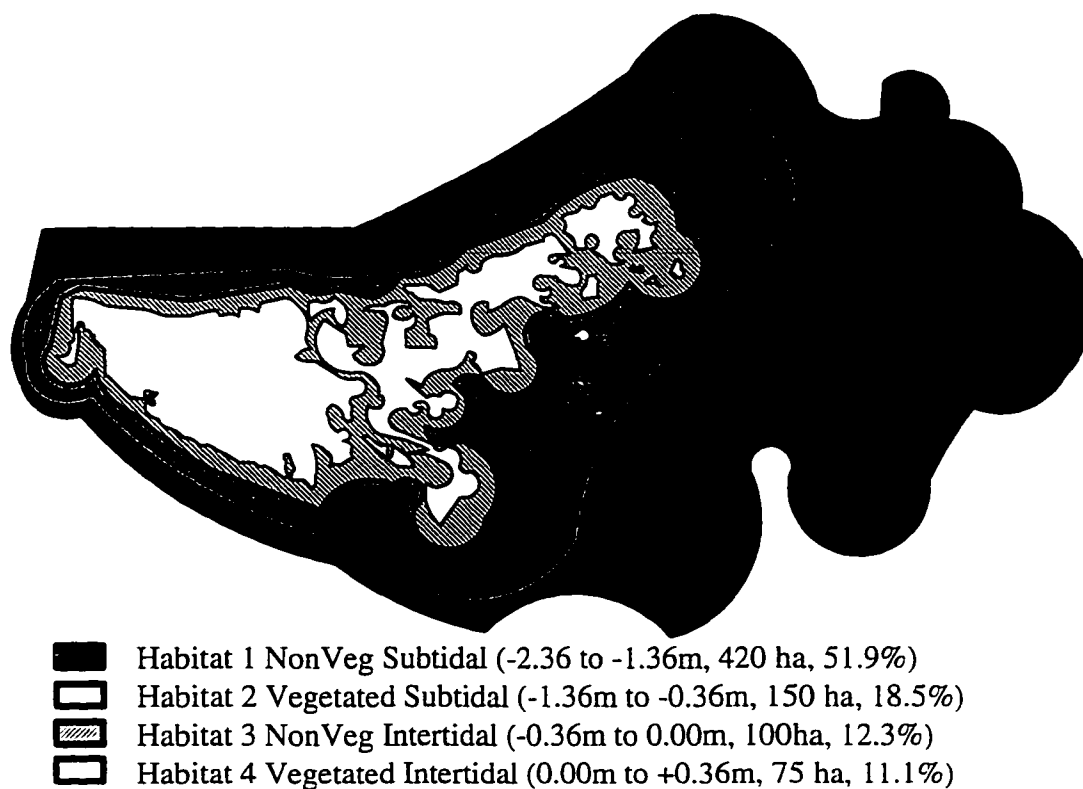
Model Description

Conceptual Design

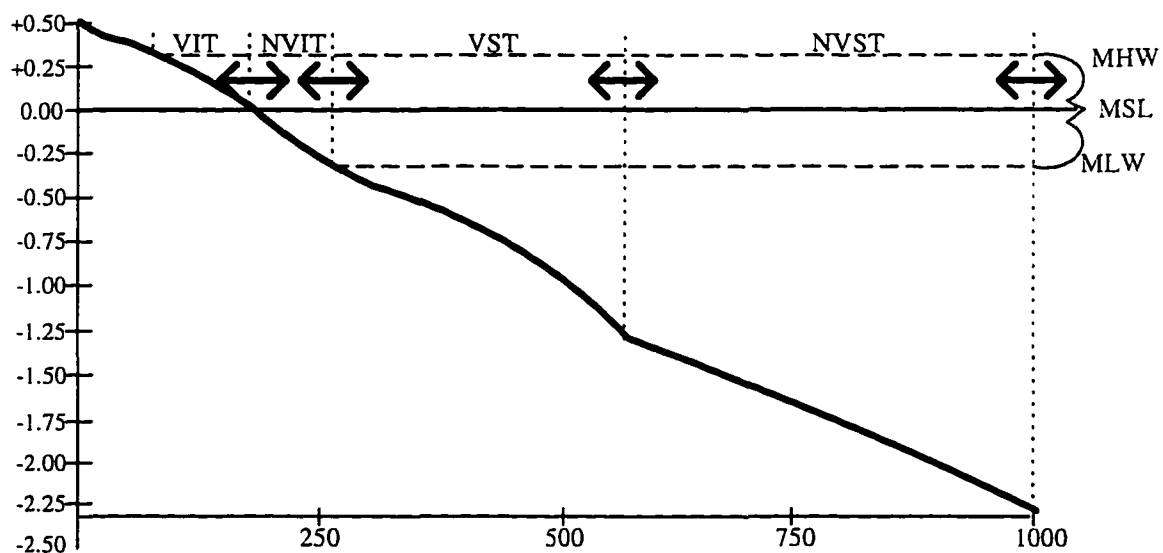
Four concentric primary habitat types were identified and include (1) nonvegetated subtidal (NVST: 420 ha), (2) vegetated subtidal (VST: 120 ha), (3) nonvegetated intertidal (NVIT: 100 ha), and (4) vegetated intertidal (VIT: 85 ha) (Fig. 1). These four habitats were selected based upon abiotic and biotic characteristics relative to the elevation gradient along which they are located (Fig. 1B; Buzzelli Section 2). Figure 2 depicts generalized conceptual diagrams for each of the 4 habitat models that were based upon the four habitat

Figure 1. (A) Habitat size and distribution map for the littoral zone of the Goodwin Islands NERR. (B) Shoreline profile for the littoral zone of the Goodwin Islands NERR.

(A) Habitat Map for the Goodwin Islands Littoral Zone



(B) Goodwin Islands shoreface profile depicting distribution of littoral zone habitats



types. The global forcing functions are tidal water level, irradiance, and water temperature. The subtidal and intertidal nonvegetated models each have 7 state variables including large and small phytoplankton size classes (diatoms and other plankton, respectively), labile and refractory particulate organic carbon (LPOC and RPOC), dissolved organic carbon (DOC), and total dissolved inorganic nitrogen (TDIN) and sediment microalgae (SM) (Table 1). In addition to these 7 state variables the vegetated subtidal and intertidal habitat models include additional state variables in the forms of epiphyte carbon (ZepiC) and shoot and root-rhizome carbon and nitrogen of *Zostera marina* or *Spartina alterniflora* (ZSC, ZSN, ZRRC, ZRRN, SSC, SSN, SRRC, SRRN; Table 1). The initial values for water column state variables in the intertidal habitats are set to zero because the model begins on an ebb tide. An Euler integration routine is used with an integration interval (dt) for the subtidal habitat models of 0.03125 d (0.75 hrs or 45 min) while intertidal habitat models use 0.0078125 d (0.1875 hrs or 11.25 min). Simulations can span 1-10 years of model time.

Mathematical Structure: Hydraulic Simulation

This is a pseudo-spatial model of a concentric series of habitats based upon an island ecosystem. The model is pseudo-spatial because the habitats are not geographically referenced but there is a specific sequence of habitats that flooding and ebbing tidal water must follow. The habitat boxes fill and drain in consecutive order with the output from one providing the input for the next in the sequence. The exchanges across habitat boundaries follow a 2-D mass balance model (Costanza et al. 1990). The nonvegetated subtidal habitat model is bounded by an unlimited source/sink representing the offshore channel while the vegetated marsh is bounded by the upland with no exchange across the upland boundary. Watershed exchanges are assumed to be zero because the Goodwin Islands have little upland and are isolated from the mainland. Upland exchanges could be easily implemented if a terrestrial linkage is desired.

Tidal water level is modeled using the largest six amplitudes of the 1993 tidal

Figure 2. Generalized conceptual diagram for the four habitat models. Dashed lines are information flows while solid lines with workgates represent mass flows. Model time, tidal water level, photosynthetically active radiation (PAR), and water temperature (Temp) are the global forcing functions. Each habitat model includes six water column state variables (DIA, OP, LPOC, RPOC, DOC, TDIN). The two phytoplankton size classes (diatoms and other plankton) and the two particulate organic carbon fractions (labile and refractory) are shown as paired state variables. PAR is attenuated by water and the concentrations of POC, DOC, and chlorophyll (Chl *a*). Each model also includes a sediment microalgae state variable (SM). The vegetated subtidal and intertidal models have carbon and nitrogen state variables for the shoots and root-rhizomes of *Zostera marina* and *Spartina alterniflora*, respectively.

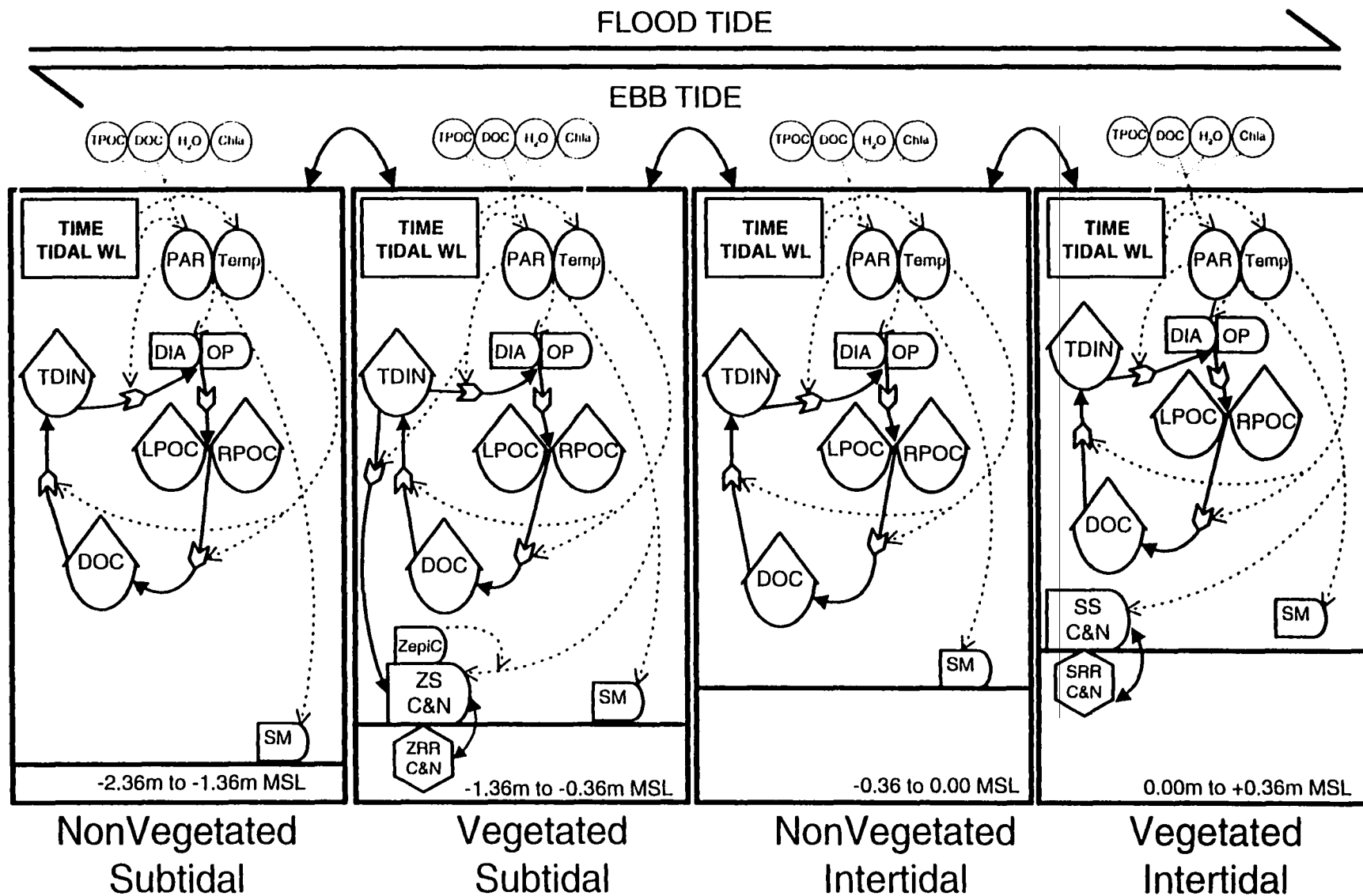


Table 1. List of state variables for habitat models. Each habitat model includes the first 7 state variables listed. In addition to the basic seven the vegetated subtidal habitat model (VST) includes those related to *Zostera marina* while the vegetated intertidal habitat model (VIT) has those related to *Spartina alterniflora*.

ABBREV.	DESCRIPTION	UNITS
DIA	Diatom Carbon Mass	gC
OP	Other Plankton Carbon Mass	gC
LPOC	Labile Particulate Organic Carbon	gC
RPOC	Refractory Particulate Organic Carbon	gC
DOC	Dissolved Organic Carbon	gC
TDIN	Total Dissolved Inorganic Nitrogen	μM
SM	Sediment Microalgae	gC m^{-2}
ZSC	<i>Zostera marina</i> Shoot Carbon	gC m^{-2}
ZSN	<i>Zostera marina</i> Shoot Nitrogen	gN m^{-2}
ZRRC	<i>Zostera marina</i> Root-Rhizome Carbon	gC m^{-2}
ZRRN	<i>Zostera marina</i> Root-Rhizome Nitrogen	gN m^{-2}
ZepiC	<i>Zostera marina</i> Epiphytic Biomass	gC m^{-2}
SSC	<i>Spartina alterniflora</i> Shoot Carbon	gC m^{-2}
SSN	<i>Spartina alterniflora</i> Shoot Nitrogen	gN m^{-2}
SRRC	<i>Spartina alterniflora</i> Root-Rhizome Carbon	gC m^{-2}
SRRN	<i>Spartina alterniflora</i> Root-Rhizome Nitrogen	gN m^{-2}

equation calculated for Gloucester Point, Virginia (D. Evans, personal communication; Table 2). The change in tidal height at each time step is multiplied by habitat wetted area to derive the changes in habitat volumes used in the simulation of water column processes (Table 2). While subtidal habitat wetted areas are constant, intertidal habitat wetted areas are derived using a hypsometric curve. This study uses hypsometry because it provides a concise method in which to represent the cumulative characteristics of basin morphology and hypsometric determination of inundation can be useful in the analysis of wetland biogeochemical cycling (Strahler, 1952; Eiser and Kjerve, 1986; Childers et al., 1993; Friedrichs and Aubrey, 1994). A linear hypsometry was assumed for the Goodwin Islands NERR because of the relatively flat nonvegetated intertidal and marsh surfaces.

The habitat volume changes and flux equations for water column masses were derived using 2-D finite difference solutions to equations for the exchange of conservative substances between a channel and an adjacent control volume for both flood and ebb conditions (K. Park, personal communication). This approach assumes no diffusion or advection and the water within each box is homogeneously mixed over each time step. To maintain mass and volume balance the outermost nonvegetated subtidal habitat must receive sufficient volume from the offshore boundary to provide for the change in its own volume in addition to that of the remaining three habitats. In order to conserve volume the same volume that enters a habitat on the flood tide must exit on the following ebb tide and the change in habitat volume ($dVol_{hab}; m^3$) is calculated as the change in tidal water level ($d\eta$) multiplied by the sum of the wetted areas of the habitats remaining in the flood tide sequence ($Area_{hab}$; Table 2). There are flood and ebb conditions for the exchange of water column DIA, OP, LPOC, RPOC, and DOC between a given habitat and its two adjacent environments. Table 2 contains the mathematical structure for the inter-habitat exchange of diatoms (DIA) as an example. Each habitat has two constant boundary conditions for each

Table 2. Mathematical formulations for tidal water level (η), habitat volume, and inter-habitat water column exchange for the four habitat models of the Goodwin Island littoral zone. Intertidal habitat depth and volume are calculated similarly as subtidal depth except that they equal zero when the intertidal habitats are not inundated. Intertidal wet area is calculated using a linear hypsometric profile. An offshore to inshore habitat sequence is denoted a, b, c and all water column state variables follow the format shown here for diatoms (DIA).

Tidal water level (η ; m)

$$\eta = \text{MSL} + (0.356 * \text{Cos}(0.5059 * \text{modhrs} - 1.583)) + (0.067 * \text{Cos}(0.5236 * \text{modhrs} - 5.039)) + (0.074 * \text{Cos}(0.4964 * \text{modhrs} + 1.264)) + (0.047 * \text{Cos}(0.2625 * \text{modhrs} - 1.854)) + (0.037 * \text{Cos}(0.2434 * \text{modhrs} + 0.332))$$

Change in Tidal Water Level ($d\eta$; m)

$$d\eta = \eta_t - \eta_{t-\Delta t}$$

Habitat Depth (h_{SThab} ; m)

$$h_{SThab} = \eta_t - z_{SThab}$$

Habitat Volume (VOL_{SThab} ; m³)

$$VOL_{SThab} = \text{Area}_{SThab} * h_{SThab}$$

Change in Habitat Volume ($dVol_{hab}$; m³)

$$dVol_{VST} = d\eta * (\text{Area}_{VST} + \text{Area}_{VST} + \text{Area}_{VST} + \text{Area}_{VST})$$

$$dVol_{VST} = d\eta * (\text{Area}_{VST} + \text{Area}_{VST} + \text{Area}_{VST})$$

$$dVol_{VST} = d\eta * (\text{Area}_{VST} + \text{Area}_{VST})$$

$$dVol_{VST} = d\eta * (\text{Area}_{VST})$$

Habitat b Diatom Exchange with Offshore Habitat a (DIA_{flxab})

$$DIA_{flxab} = dVol_b * DIAc_a \quad (\text{If } d\eta > 0.0)$$

$$DIA_{flxab} = dVol_b * DIAc_b \quad (\text{If } d\eta < 0.0)$$

Habitat b Diatom Exchange with Inshore Habitat c (DIA_{flxba})

$$DIA_{flxba} = dVol_c * DIAc_b \quad (\text{If } d\eta > 0.0)$$

$$DIA_{flxba} = dVol_c * DIAc_c \quad (\text{If } d\eta < 0.0)$$

water column constituent (Appendix b). On a flooding tide ($d\eta > 0.0$), the exchange of materials between the offshore habitat boundary a and habitat b (DIA_{flxab}) is calculated as the change in volume of habitat b ($dVol_b$) multiplied by the incoming diatom concentration a ($DIAc_a$; $gC\ m^{-3}$). On an ebbing tide ($d\eta < 0.0$) the exchange of diatoms between habitat b and offshore habitat boundary a (DIA_{flxba}) is calculated as the change in the volume of habitat b ($dVol_b$) multiplied by the diatom concentration leaving habitat b ($DIAc_b$; $gC\ m^{-3}$).

Mathematical Structure: State Variables

Table 3 contains the system of differential equations used to model the changes in the state variables listed in Table 1. Primary production ($gC\ m^{-2}$ or $m^{-3}\ d^{-1}$) is modeled from the combination of gross production, respiration, and loss through mortality or grazing. Phytoplankton (DIA and OP) are also influenced by exudation, sedimentation, and transport to adjacent habitats (Table 3). The mathematical representations of production and photosynthesis control in other plankton, sediment microalgae, and *Spartina alterniflora* are all similar to the diatom (DIA) examples provided in Appendix a. Gross production is a function of irradiance, temperature, and dissolved inorganic nitrogen (Table 3). Incident photosynthetically active radiation (PAR_0 ; $\mu E\ m^{-2}\ s^{-1}$) is calculated from an empirical curve fit for Gloucester Point, VA (Wetzel and Meyers, 1994). Submarine PAR (PAR_z ; $\mu E\ m^{-2}\ s^{-1}$) is attenuated using an exponential decay function with depth and the total attenuation coefficient (k_d) is summed from the attenuation due to water and the concentrations of chlorophyll *a*, total POC, and DOC (Keller, 1988; Keen and Spain, 1992; McPherson and Miller, 1987). In the vegetated subtidal and intertidal habitat models the PAR that reaches the sediment surface is attenuated by macrophyte canopy

Table 3. System of differential equations for state variables listed in Table 1.

Diatom Carbon Mass (gC)

$$DIA_{hab(t)} = DIA_{(t-dt)} + (DIA_{prod} - DIA_{resp} - DIA_{mort} - DIA_{exu} - DIA_{sed} \pm DIA_{flxab} \pm DIA_{flxbc}) * dt$$

Other Plankton Carbon Mass (gC)

$$OP_{hab(t)} = OP_{(t-dt)} + (OP_{prod} - OP_{resp} - OP_{mort} - OP_{exu} - OP_{sed} \pm OP_{flxab} \pm OP_{flxbc}) * dt$$

Labile Particulate Organic Carbon (gC)

$$LPOC_{hab(t)} = LPOC_{(t-dt)} + (LPOC_{prod} - LPOC_{hydrol} - LPOC_{sed} \pm LPOC_{flxab} \pm LPOC_{flxbc}) * dt$$

Refractory Particulate Organic Carbon (gC)

$$RPOC_{hab(t)} = RPOC_{(t-dt)} + (RPOC_{prod} - RPOC_{hydrol} - RPOC_{sed} \pm RPOC_{flxab} \pm RPOC_{flxbc}) * dt$$

Dissolved Organic Carbon (gC)

$$DOC_{hab(t)} = DOC_{(t-dt)} + (DOC_{prod} - DOC_{remain} \pm DOC_{flxab} \pm DOC_{flxbc}) * dt$$

Total Dissolved Inorganic Nitrogen (μM)

$$TDIN_{hab(t)} = TDIN_{(t-dt)} + (TDIN_{prod} - TDIN_{uptake} \pm TDIN_{wily} \pm TDIN_{flxab} \pm TDIN_{flxbc}) * dt$$

Sediment Microalgae (gC m⁻²)

$$SMC_t = SMC_{(t-dt)} + (SMC_{prod} - SMC_{resp} - SMC_{lys} - SMC_{res}) * dt$$

Zostera marina Shoot Carbon (gC m⁻²)

$$ZSC_t = ZSC_{(t-dt)} + (ZSC_{prod} - ZSC_{resp} - ZSC_{lys} - ZC_{trans}) * dt$$

Zostera marina Shoot Nitrogen (gN m⁻²)

$$ZSN_t = ZSN_{(t-dt)} + (ZSN_{uptake} + ZN_{trans} - ZSN_{lys}) * dt$$

Zostera marina Root-Rhizome Carbon (gC m⁻²)

$$ZRRC_t = ZRRC_{(t-dt)} + (ZC_{trans} - ZRRC_{resp} - ZRRC_{lys} - ZRRC_{bed}) * dt$$

Zostera marina Root-Rhizome Nitrogen (gN m⁻²)

$$ZRRN_t = ZRRN_{(t-dt)} + (ZRRN_{uptake} - ZN_{trans} - ZRRN_{lys} - ZRRN_{bed}) * dt$$

Zostera marina Epiphytic Biomass (gC m⁻²)

$$ZepiC_t = ZepiC_{(t-dt)} + (ZepiC_{prod} - ZepiC_{resp} - ZepiC_{graz} - ZepiC_{lys}) * dt$$

Spartina alterniflora Shoot Carbon (gC m⁻²)

$$SSC_t = SSC_{(t-dt)} + (SSC_{prod} - SSC_{resp} - SSC_{lys} \pm SC_{trans}) * dt$$

Spartina alterniflora Shoot Nitrogen (gN m⁻²)

$$SSN_t = SSN_{(t-dt)} + (SN_{trans} - SSN_{lys}) * dt$$

Spartina alterniflora Root-Rhizome Carbon (gC m⁻²)

$$SRRC_t = SRRC_{(t-dt)} + (SC_{trans} - SRRC_{resp} - SRRC_{lys} - SRRC_{bed}) * dt$$

Spartina alterniflora Root-Rhizome Nitrogen (gN m⁻²)

$$SRRN_t = SRRN_{(t-dt)} + (SRRN_{uptake} - SN_{trans} - SRRN_{lys} - SRRN_{bed}) * dt$$

Biomass (Pinckney and Zingmark, 1993b; Morris, 1989). Respiration follows an exponential relationship with temperature while production and mortality are similar to those in Cerco and Cole (1994; appendix a). Phytoplankton exudation is modeled as a constant fraction of production and sedimentation is calculated from the phytoplankton mass, the sedimentation constant, and the habitat depth (Cerco and Cole 1994; appendix a). Phytoplankton nitrogen demand is calculated using the daily net primary productivity rate and the Redfield C:N ratio and nitrogen uptake by diatoms and other plankton is calculated following the assumptions and parameters of Michaelis-Menten kinetics (appendix a). The maximum photosynthetic rate (SMP_{max}) and the half-saturation irradiance (SMIK) of sediment microalgae were calculated from data provided in Pinckney and Zingmark (1993a). A constant fraction of sediment microalgae are lost through resuspension and are grazed with the square of the biomass (appendix a).

Appendix b lists all of the parameters, boundary conditions, and constants used in the four habitat models. The values listed were derived from a variety of published and unpublished data, response plots, and calibration runs. While there are sufficient data related to water column concentrations (except DOC) and *Zostera marina* in lower Chesapeake Bay to accomplish both model calibration and validation, data related to sediment microalgae and *Spartina alterniflora* are not as abundant. Equations from Cerco and Cole (1994) were used to model the dynamics of DIA and OP, TPOC, DOC, and TDIN and these state variables were calibrated and initialized following information provided in Batuik et al. (1992) for subtidal habitat models and Childers, et al. (1993) for intertidal habitat models. *Zostera marina* biomass output and the equations that represent nitrogen processes in *Zostera marina* were calibrated using the data of (Buzzelli, 1991; Buzzelli and Wetzel, in review). Data from the literature and the biomass data collected at the Goodwin Islands NERR (Buzzelli Section 2) were used to calibrate microalgal and *Spartina alterniflora* rate processes and model biomass. The maximum photosynthetic rate

of *Spartina alterniflora* was calculated based upon data from a variety of sources (Blum et al., 1978; Drake and Read, 1981; Morris, 1982; Morris et al. 1984; Pezeshki et al., 1987; Morris and Bradley, 1990). The equations for nitrogen relationships in *Spartina alterniflora* were calibrated using the data and equations of Hopkinson and Schubauer (1984) and Morris (1982), respectively. Equations for carbon translocation and root-rhizome metabolic processes in *Spartina alterniflora* were derived using information found in Morris et al. (1984).

Water column particulate organic carbon (POC; gC m^{-3}) is influenced by production, hydrolysis, settling, and exchange between adjacent habitats (Table 3). POC is produced from a fraction of phytoplankton and resuspended sediment microalgae (appendix a). POC is divided into labile and refractory fractions and the rates of hydrolysis are calculated using an exponential relationship with temperature (Cercio and Cole 1994). LPOC and RPOC both settle from the water column (appendix a) and are exchanged laterally (see Table 2 DIA exchange examples). DOC is influenced by production, remineralization, and exchange with adjacent habitats (Table 3). Hydrolyzed POC provides the DOC production rate while the remineralization rate is controlled by a temperature function and the refractory DOC fraction (appendix a; Cercio and Cole, 1994). Water column TDIN (mmoles m^{-3}) is influenced by production, autotrophic uptake, sediment-water fluxes, and exchange with adjacent habitats (Table 3). Production is calculated using the DOC remineralization rate and the C:N ratio of dissolved organic matter (appendices a and b). TDIN is removed from the water column through uptake by phytoplankton in all habitat models and by *Zostera marina* in the vegetated subtidal habitat model (appendix a). During the day TDIN is exchanged vertically between the sediment and the overlying water column based upon rates determined from core incubations in subtidal (Buzzelli Section 2) and intertidal habitats (Neikirk, 1996) while at night there is

zero vertical exchange of DIN.

The formulations for carbon productivity by *Zostera marina* shoots and epiphytes have been provided elsewhere (Wetzel and Neckles, 1986; Wetzel and Meyers, 1994). A constant fraction of shoot net production is translocated downward in *Zostera marina* but the process is limited by a feedback function based upon the maximum and limiting biomass values (ZSCfb, Appendix b; Wetzel and Neckles, 1986). *Zostera marina* root-rhizomes respire following an Arrhenius relationship with temperature (Park and Kuo, 1993; Bach, 1993). Nitrogen uptake by the shoots and root-rhizomes of *Zostera marina* are modeled using Michaelis-Menten saturation limited by feedback functions based on the maximum and minimum nitrogen contents of the shoot and root-rhizome tissues (appendices a and b). Nitrogen uptake equals zero at night and *Zostera marina* shoots and root-rhizomes C and N are balanced through the proportional nitrogen loss terms. Nitrogen is translocated only from root-rhizomes to shoots in order to meet shoot nitrogen demand (appendix a). Nitrogen translocation is also limited by feedback functions based on the maximum and minimum nitrogen contents of the source (RR) and target (shoot) tissues (ZSCNfb, appendix b).

Shoot and root-rhizome respiration in *Spartina alterniflora* are modeled using the Arrhenius representation (Park and Kuo, 1993; Bach, 1993). A constant fraction of shoot net production (SCPot in appendix b) is translocated downward to the root-rhizome carbon pool except in the spring and fall. In the spring a pulse of root-rhizome carbon is translocated up to the shoots to initiate growth (appendix b). A senescence function moves a majority of the shoot carbon downwards in the late fall for belowground storage. The formulations for nitrogen state variables of *Spartina alterniflora* are similar to those of *Zostera marina* except that there is no shoot uptake of nitrogen in *Spartina alterniflora*.

Model Sensitivity Analysis

There are a large number of factors that could potentially influence the resulting state variable concentrations (appendix b). The sensitivities of the model state variables to the various parameters were investigated using a systematic series of model trial runs. Analyses included a particular state variable over successive years of the same model run as well as the comparison of year two results among a series of different sensitivity runs. Four to six individual ecological parameters were selected for each state variable listed in Table 1 to analyze their effects upon the resulting model concentration over year two of simulation. Each parameter was varied by +10% and -10% in individual runs and the root mean square deviation (RMS) between the stable, nominal model case and the sensitivity run was calculated (Cerco, 1993).

$$RMS = \sqrt{\frac{1}{n} \sum_{i=1}^n (P_i - O_i)^2}$$

Where P_i = model nominal run, O_i = sensitivity run, and n = number of dt in year two simulation ($n=5840$). The RMS was compared to the average state variable concentration of the nominal run to determine the percent change in concentration due to parameter effects. In the cases of the carbon state variables of *Zostera marina* and *Spartina alterniflora*, the potential interactions between two or three varied parameters were investigated for year two output.

Model Validation

Validation data from the Goodwin Islands were available only for particular model state variables. Graphical validation was performed for the second year of water column chlorophyll a, total particulate organic carbon (TPOC), and total dissolved inorganic nitrogen (TDIN) output from the vegetated subtidal habitat models. Graphical validation

was also performed for the shoot, root-rhizome, and epiphyte carbon state variables of *Zostera marina*. The output for all of these state variables was compared to data collected at the Goodwin Islands by Moore et al. (1994). *Spartina alterniflora* shoot and root-rhizome carbon biomass were validated using data assembled from the literature (Mendelssohn, 1973; Smith et al., 1979; Ornes and Kaplan, 1989; Gross et al., 1991). There are no data available at this time to validate model representation of patterns of littoral zone water column DOC dynamics, sediment microalgal production and biomass, and habitat specific and inter-habitat variations in sediment-water and horizontal material exchanges.

RESULTS

Model Sensitivity Analysis

DIA, LPOC, and SM of the VST model were only marginally sensitive to two parameters each as a 10% change in a parameter triggered only 5-10% change in average biomass (Table 4). A 10% change in the basal metabolic respiration rate of *Zostera marina* epiphytes (BMRZepi) created a 37% change in the year two average biomass. Half-saturation irradiance (ZIK), the shoot fall mortality coefficient (ZSFMK), and the translocation potential (ZCPot) had the biggest effects of the *Zostera marina* parameters tested. Shoot and root-rhizome biomass varied by approximately 9% with a $\pm 10\%$ change in the half-saturation irradiance (ZIK; Table 4). A $\pm 10\%$ change in the shoot fall mortality coefficient (ZSFMK) created a 11-13% change in the shoot and root-rhizome biomass while changing the translocation potential (ZCPot) had a very small effect on the shoots (1.94%) and a larger effect on the root-rhizome biomass (8.06%; Table 4). Only the combination of increased half-saturation irradiance (ZIKH and L) and shoot fall mortality coefficient (ZSFMKH and L) appeared to interact and decreased the shoot and root-rhizome biomass by approximately 25% (Table 4).

Spartina alterniflora shoot and root-rhizome biomass were greatly influenced by

Table 4. The results of sensitivity analysis for diatom (DIA), labile particulate organic carbon (LPOC), sediment microalgae (SM), and carbon state variables for *Zostera marina* shoots (ZSC), root-rhizomes (ZRRC), and epiphytes (ZepiC) of the vegetated subtidal habitat model (VST model is #2). Refer to appendix b for parameter definitions and values. The root mean square deviation (RMS) was calculated as the difference in state variable concentrations between nominal (accepted) and sensitivity runs performed under +10% and -10% parameter changes. The percent change (%) is the average change in state variable concentration given a $\pm 10\%$ change in parameter value.

VARIABLE	PARAMETER	AVERAGE RMS	%CHANGE
DIA2c	DIASdK	0.004	5.45
	PRRd	0.002	2.30
LPOC2c	FLPOC	0.137	10.5
	DetStdV	0.068	5.20
SM2C	SMIK	0.106	6.04
	SMResK	0.112	6.41
ZEpiC	BMRZepi	3.650	37.7
	ZepiGK	0.871	8.99
ZSHC	ZIK	3.927	9.25
	ZSFMK	5.482	12.9
	ZCpot	0.826	1.94
ZRRC	ZIK	1.156	9.32
	ZSFMK	1.341	10.8
	ZCpot	1.000	8.06
ZSHC	ZCpotH&ZIKL	4.727	11.1
	ZCpotH&ZSFMKL	3.389	7.98
	ZIKH&ZSFMKH	8.369	19.7
	ZIKL&ZSFMKL	10.521	24.8
ZRRC	ZCpotH&ZIKL	0.404	3.26
	ZCpotH&ZSFMKL	0.852	6.87
	ZIKH&ZSFMKH	2.469	19.9
	ZIKL&ZSFMKL	3.093	24.9

10% changes in the maximum photosynthetic rate (SPmax), the root-rhizome respiration rate at 20 °C (SRRR@20), and the translocation potential (SCPot; Table 5). A 10% increase in SPmax increased shoot biomass by an average of 53% and root-rhizome biomass by 32% during the second year of output from the VIT model. The effect of increased SPmax upon shoot and root-rhizome biomass over 3 model years is shown in Figure 3A. A $\pm 10\%$ change in the SRRR@20 created a 95% change in shoot biomass and a 27% change in root-rhizome biomass (Table 5). Shoot carbon biomass was also quite sensitive to changes in SCPot (73.4%) while the root-rhizome biomass displayed effects similar to those of SRRR@20 (Table 5). The shoot respiration rate at 20 °C (SSR@20) and the shoot basal mortality rate (SSC_{bmort}) elicited individual effects that were greatly reduced relative to SPmax, SRRR@20, and SCPot (Table 5). Paired combinations of parameters were also tested and the effects of SPmax were prevalent (Table 5). The combination of increased SPmax and increased root-rhizome basal respiration provided a 61% increase in average shoot biomass (Fig. 3B). The effects of SPmax could be mitigated by changing the translocation potential (SCPot; Table 5 and Fig. 3C). The effects of increased rates of photosynthesis, translocation, and root-rhizome respiration upon shoot and root-rhizome biomass were analyzed and again the effects of increased SPMax were mitigated by changing the other parameters (Table 5). The cumulative effects of this combination reduces average shoot biomass by approximately 29% and root-rhizome biomass by only 2.6%.

Validation

Subtidal Water Column Concentrations

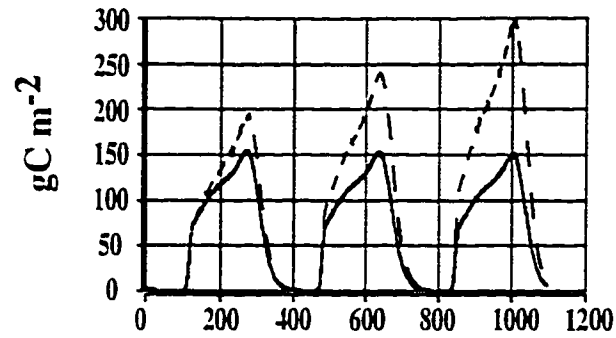
The modeled concentrations of chlorophyll *a*, total POC (labile + refractory), and TDIN in the water column of the vegetated subtidal habitats were validated using data

Table 5. The results of sensitivity analysis for *Spartina alterniflora* shoot and root-rhizome carbon state variables (SSC and SRRC) from the vegetated intertidal habitat model (VIT). Refer to appendix b for parameter definitions and values. The root mean square deviation (RMS) was calculated as the difference in state variable concentrations between nominal (accepted) and sensitivity runs performed under +10% and -10% parameter changes. The percent change (%) is the average change in state variable concentration given a $\pm 10\%$ change in parameter value.

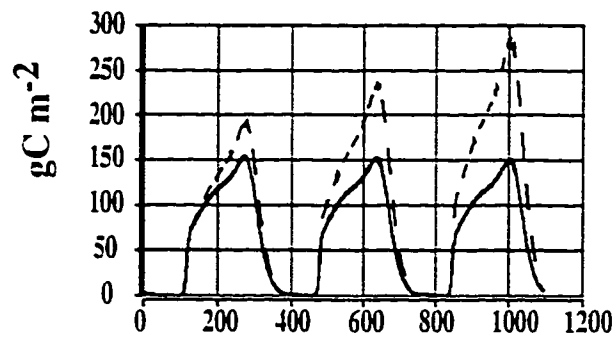
VARIABLE	PARAMETER	AVERAGE RMS	%CHANGE
SSC	SPMax	35.48	53.4
	SRRR@20	63.32	95.3
	SCpot	48.77	73.4
	SSR@20	11.96	18.0
	SSC _{bmort}	6.88	10.4
SRRC	SPMax	184.1	31.9
	SRRR@20	154.1	26.7
	SCpot	125.3	21.7
	SSR@20	60.74	10.5
	SSC _{bmort}	25.73	4.45
SSC	SPmaxH&SRRR@20H	40.27	60.6
	SpmaxL&SRRR@20L	25.97	39.1
	SPmaxH&SCpotH	17.30	26.0
	SSR@20H&SCpotH	35.77	24.8
SRRC	SPmaxH&SRRR@20H	192.0	33.4
	SpmaxL&SRRR@20L	127.9	22.2
	SPmaxH&SCpotH	72.7	12.6
	SSR@20H&SCpotH	131.3	22.8
SSC	SpmaxH,SCPotH, SRRR@20H	19.07	28.7
SRRC	SpmaxH,SCPotH, SRRR@20H	15.01	2.6

Figure 3. Sensitivity results for shoot carbon biomass (gC m^{-2}) of *Spartina alterniflora*. The effects of the maximum photosynthetic rate (SPMax) are shown as a single factor in (A), as a two-way factor with increased root-rhizome basal respiration rate (SRRR@20) in (B), and as a two-way factor with the carbon translocated potential included (SCPotH) in (C). The nominal run is shown as the solid line and the sensitivity run is shown as the dashed line.

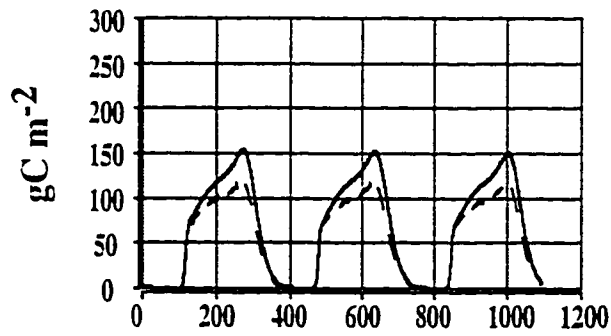
(A) SPmaxH vs Nominal (—)



(B) SPmaxH & SRRR@20H vs Nominal (—)



(C) SPmaxH, and SCPotH vs Nominal (—)



Julian Day

collected during intensive field studies conducted at the Goodwin Islands NERR 7-17 June 1993 (Fig. 4; Moore et al., 1994). Figure 4 A-C depict the relationships between the field data and concentrations output from the VST model. The flood/ebb signal is explicit in the model but not as obvious in the field data where the effects of miscellaneous changes in habitat volume (e.g. wind events) are superimposed on the tidal signal to produce the observed patterns. VST model chlorophyll *a* is approximately 5 mg m^{-3} while the field data was scattered between 5 and 25 mg m^{-3} (Fig. 4A). Vegetated subtidal model concentrations of TPOC ranged between 1 and 3 gC m^{-3} and are within the range of values recorded in the field (Fig. 4B). There was synchronization in the TPOC concentrations between the model and field data from June 8 to June 12 but there was a resuspension event around June 13 or 14 (Fig. 4B). Water column TDIN concentrations from the VST model are within range of field data during the first few days of simulation but decline to very low values beginning around 11 June (Fig. 4C). There was some variability in the TDIN concentrations measured in the field (0-5 μM).

Zostera marina Biomass

Graphical validation of *Zostera marina* shoot, root-rhizome, and epiphytic biomass are shown in Figure 5. The validation data were collected at the Goodwin Islands NERR in 1993 (Moore et al., 1994). The model sufficiently represents the annual patterns in the biomass of these three state variables. While the model predicts summer shoot biomass of approximately 30 gC m^{-2} , actual shoot biomass was below 20 gC m^{-2} (Fig. 5A). Predicted root-rhizome biomass is consistent with field data except for the large peak in biomass recorded at the Goodwin Islands NERR in April 1993 (Fig. 5B; Orth and Moore, 1986). Although there were not as much data collected for epiphytic biomass at the Goodwin Islands NERR, model output is within range and agrees with other data

Figure 4. Validation results for water column constituents of the vegetated subtidal habitat model. Model results (line) are shown relative to field data collected at in the seagrass meadow during intensive studies conducted in June 1993 (Moore et al. 1994). (A) Chlorophyll *a* , (B) Total Particulate Organic Carbon (TPOC), (C) Total Dissolved Inorganic Nitrogen (TDIN).

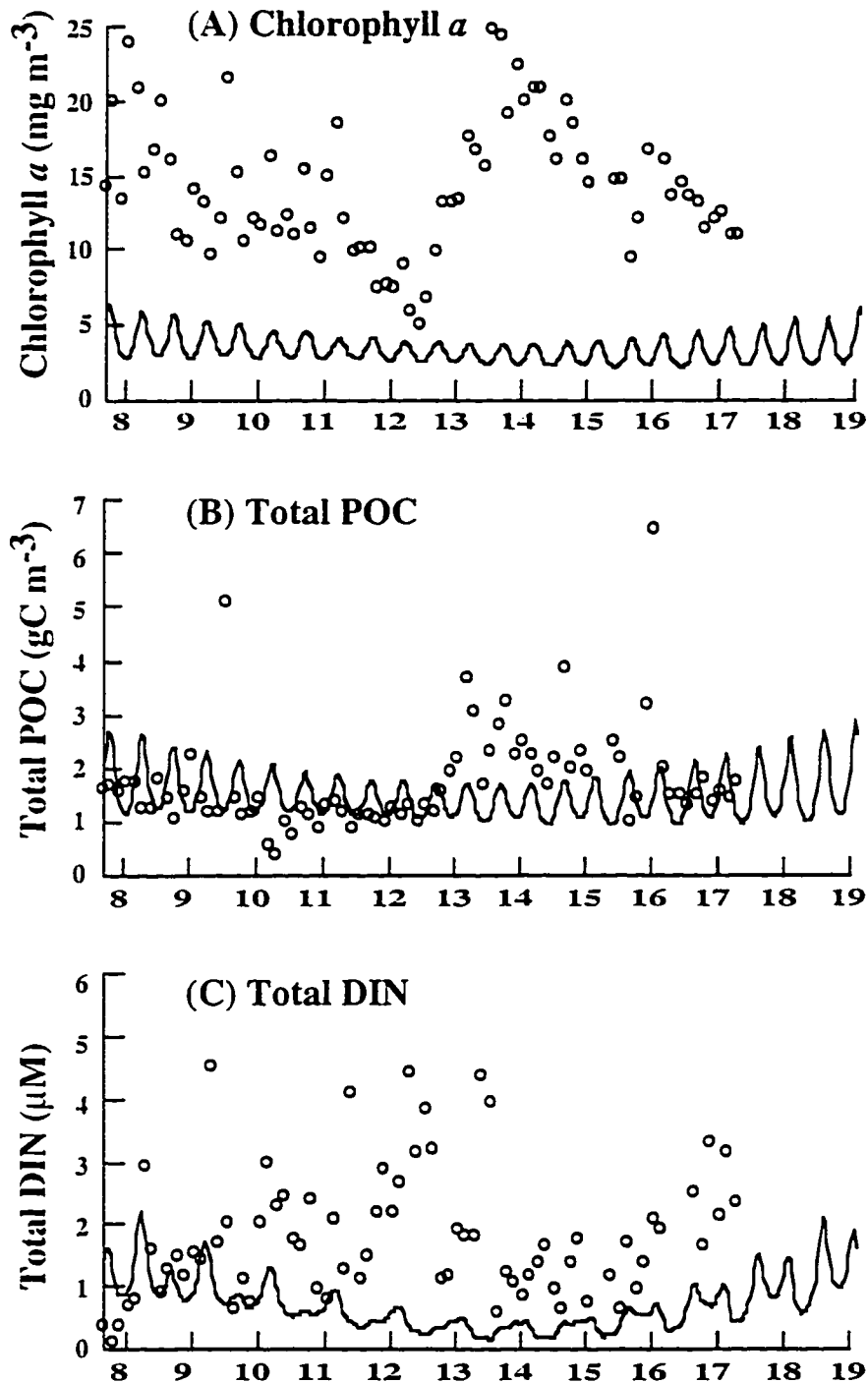
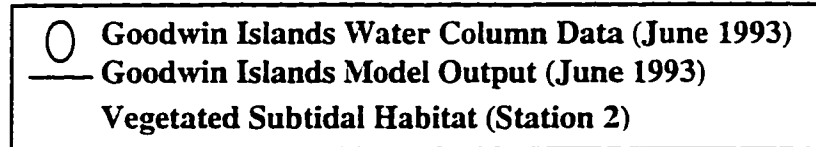


Figure 5. Validation results for carbon state variables (gC m^{-2}) representing *Zostera marina* shoot (A), root-rhizome (B), and epiphytic (C) biomass for the vegetated subtidal habitat model (VST) of the Goodwin Islands NERR.

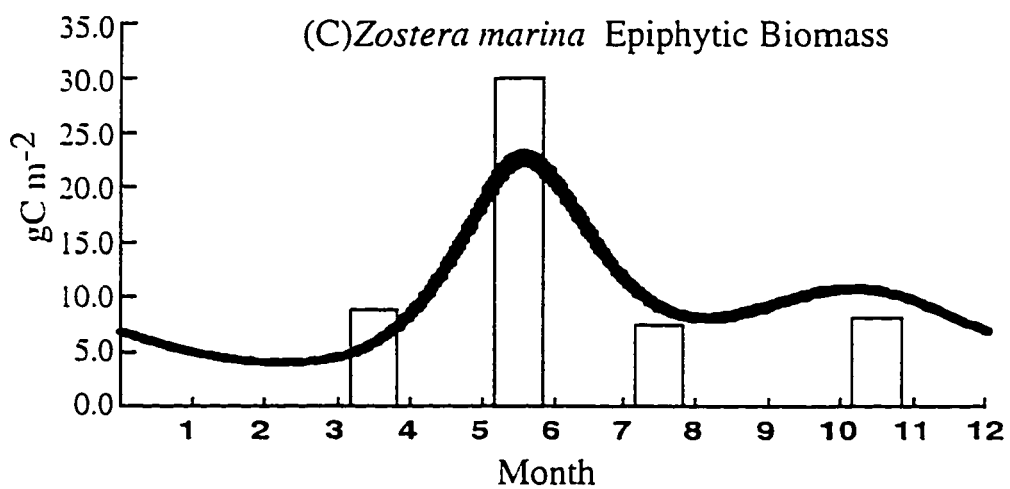
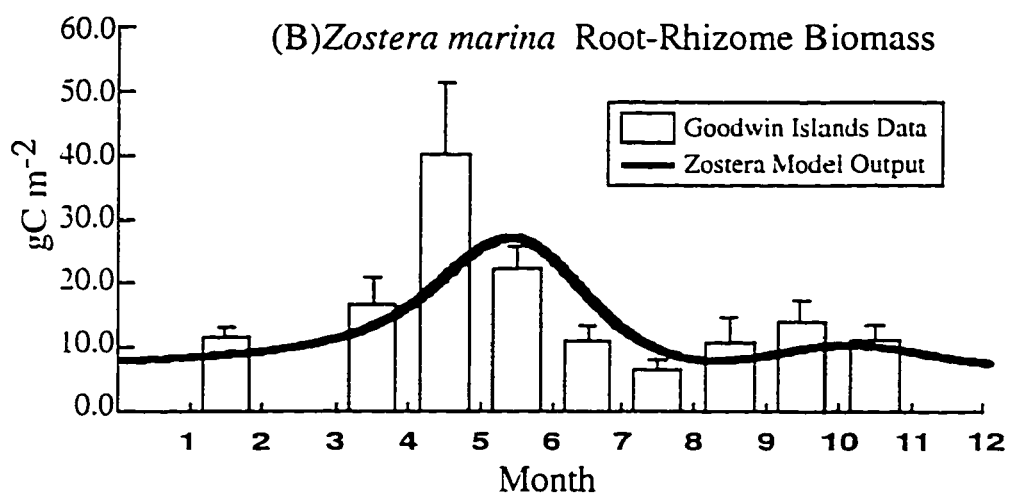
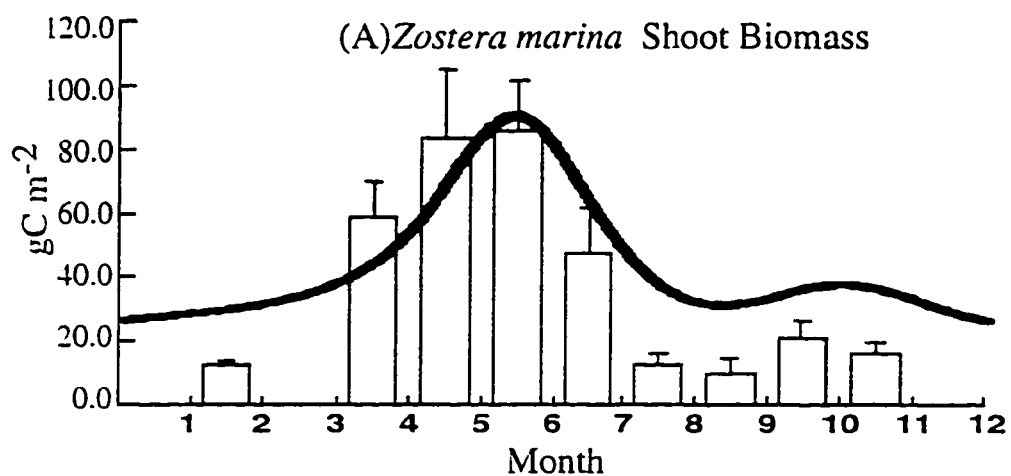
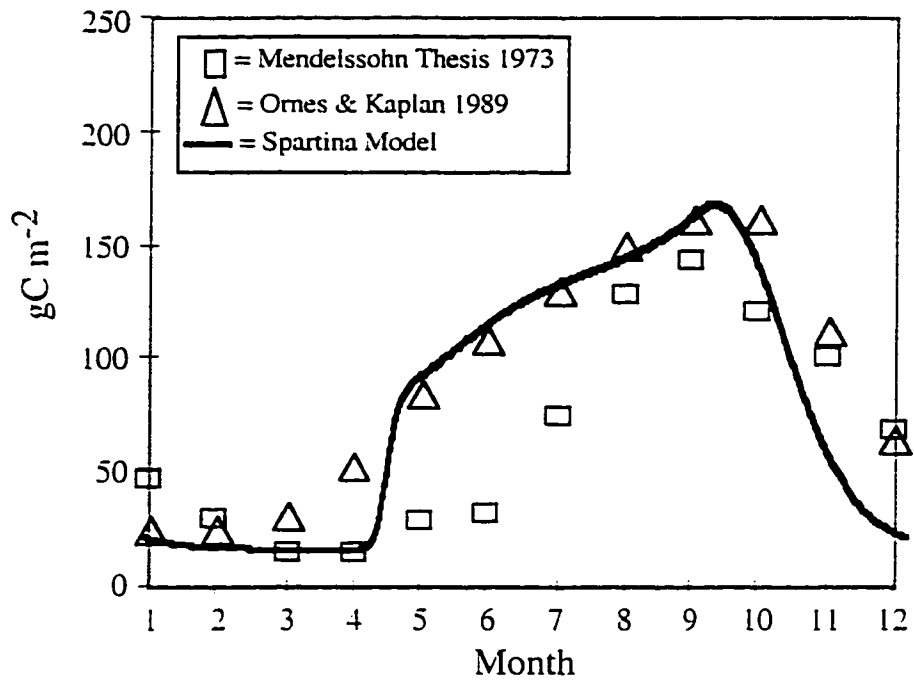
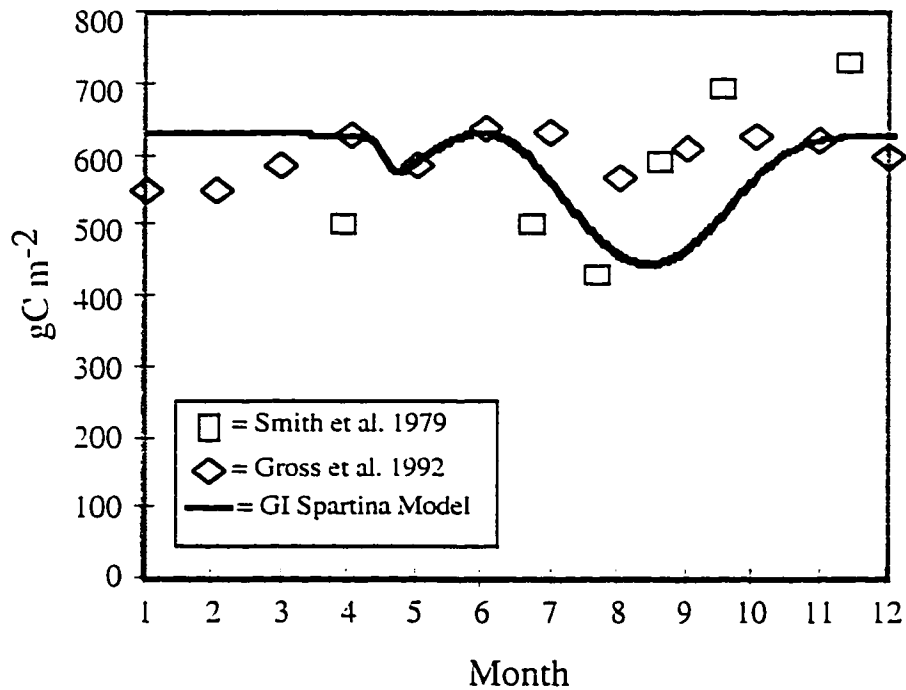


Figure 6. Validation results for carbon state variables (gC m^{-2}) representing *Spartina alterniflora* shoot (A) and root-rhizome (B) biomass for the vegetated intertidal habitat model (VIT) of the Goodwin Islands NERR.

(A) *Spartina alterniflora* Shoots



(B) *Spartina alterniflora* Root-Rhizomes



collected in the York River, Virginia (Moore, pers. Comm.).

Spartina alterniflora Biomass

The model was developed and calibrated using field data collected at the Goodwin Islands NERR (Buzzelli Section 2) and the annual patterns in shoot and root rhizome biomass of *Spartina alterniflora* generated by the model were validated with data assembled from the literature (Fig. 6). Shoot biomass was compared to data from the York River, Virginia and South Carolina (Mendelssohn, 1973; Ornes and Kaplan, 1989) while the root-rhizome output was validated with data collected in New Jersey and Delaware (Smith et al., 1979; Gross et al., 1991). Shoot carbon biomass was initialized at 3 gC m^{-2} and stays low until the spring pulse of carbon translocated from below ground (Fig. 6A; Appendix A). Root-rhizome carbon biomass was initialized at 635 gC m^{-2} and dips in April because of the upward pulse (Fig. 6B). Both shoot and root-rhizome carbon biomass rises through May and June but while the shoot continues towards a maximum of 160 gC m^{-2} by early September, the root-rhizome carbon declines during the summer owing to increased below ground respiration with temperature (Fig. 6). Shoot carbon biomass shows a steep decline in the fall as carbon is translocated below ground to the root-rhizome pool as both state variables return to their initial values. Shoot carbon biomass from the model seems to agree with field data from South Carolina (Ornes, 1989) while root-rhizome carbon biomass is within range of data reported for other marshes at similar latitude as Chesapeake Bay (Smith et al., 1979; Gross et al., 1991).

DISCUSSION

This study utilizes a unique and innovative approach to the analysis of coastal zone ecosystem dynamics. The model series was organized and developed based upon differences in sediment elevation and biotic composition among concentric littoral zone

habitats of the Goodwin Islands National Estuarine Research Reserve in Virginia (Buzzelli Section 2). These models have been used to integrate research methods (field and geographic data collection), to link distinct aquatic habitats within the ecosystem mosaic, and to link water quality and living resources in the analysis of ecosystem dynamics. The models also provide a framework to assemble available data, identify missing information, estimate ecosystem and habitat productivity, and investigate the potential impacts of altered environmental factors upon ecosystem dynamics in the Chesapeake Bay littoral zone.

These models use habitat wetted area and depth to calculate changes in habitat volume. While the subtidal models assume constant wetted area and depth is never zero, the intertidal models have variable wetted area and times of zero depth. To account for variable inundation the intertidal models use conditional statements (IF..THEN..ELSE) to calculate wetted area, depth, and water column concentration at each time step. The use of discreet conditional statements can lead to confusing results if the integration interval (dt) is too large. Because the marsh is not inundated some of the time, a large dt causes very large and sudden changes in flooded area and tidal prism volume. These effects are mitigated when dt is reduced to time scales consistent with those that regulate changes in tidal height (minutes). A smaller dt creates smoother hypsometric and volume curves to calculate changes in marsh inundation and tidal volume. Smoother changes in habitat inundation and volume provide for smoother changes in water column constituent concentration. Based upon considerations of model complexity and output, computer time, and the ranges of field data, an integration interval of 0.0078125 d (11.25 min) was chosen for the intertidal habitat models.

The concentrations of DLA, LPOC, and SM in the vegetated subtidal model are very robust with respect to 10% changes in key controlling parameters because most of the mathematical expressions for these state variables have been calibrated and utilized for a number of years (Cerco and Cole, 1994; Kuo and Park, 1994). In most cases the

concentrations of water column chlorophyll *a* , TPOC, and TDIN output by the vegetated subtidal models are consistent with data recorded at the Goodwin Islands NERR (Moore et al., 1994). These data are also within range of long term measurements made in the lower York River (Batuik et al., 1992). Model chlorophyll *a* concentrations are lower than those predicted for the surface waters of the mainstem Chesapeake Bay (10-20 mg m⁻³; Cerco, 1993). The TPOC concentrations from the Goodwin Islands subtidal habitat models are similar to those reported in Cerco (1993). The TDIN concentrations from the subtidal models are within range of the surface and bottom values predicted in Cerco (1993). The concentrations of the water column constituents in a particular habitat model are highly interrelated as phytoplankton production goes to TPOC, TPOC is hydrolyzed to DOC, DOC is remineralized to TDIN, and TDIN concentration limits phytoplankton productivity (Table 3 and appendix a).

Model simulation of *Zostera marina* shoot, root-rhizome, and epiphytic biomass were also fairly robust during sensitivity analysis although epiphytic biomass could change by 40% if its basal metabolic rate is increased or decreased by 10% (Table 4). The model approximates the annual changes in *Zostera marina* biomass and has been used to estimate net annual primary production for eelgrass meadows of lower Chesapeake Bay (Buzzelli Section 4). The equations that represent *Spartina alterniflora* are highly parameterized and the shoot and root-rhizome carbon biomass are sensitive to changes in shoot maximum photosynthetic rate (SPMax), the root-rhizome basal respiration rate (SRRR@20), and the carbon translocation potential (SCPot; Table 5). The connectivity between above and below ground carbon pools is demonstrated by the effects of these three parameters upon both shoot and root-rhizome carbon state variables. A fraction of net shoot production is translocated downward, a pulse of carbon is translocated upwards in the spring, and the remaining shoot carbon is translocated to the root-rhizomes in the fall. SPmax appears to

Table 6. Comparison of *Spartina alterniflora* maximum photosynthetic rates (d⁻¹) calculated from literature sources. The research method referenced in the literature source is provided. A 12 hour day was used to convert between hourly and daily rates.

METHOD	RATE (d ⁻¹)	SOURCE
Gas flux chambers	0.01 ^a	Blum et al., 1978
Gas flux chambers	0.13 ^b	Giurgevich and Dunn, 1979
Gas flux chambers	0.04 ^c	Drake and Read, 1981
Curve fit from growth study	0.26 ^d	Morris, 1982
Gas flux chambers	0.36 ^e	Morris et al., 1984
Gas flux chambers	0.06 ^f	Pezeshki et al., 1987
Nitrogen uptake experiments	0.36 ^g	Morris and Bradley, 1990
Goodwin Islands model	0.15 ^h	This study

^aEstimated using 0.4 gC gdw⁻¹ and 1045 gdw m⁻².

^bEstimated empirically from data provided.

^cEstimated using 0.4 gC gdw⁻¹ and 500 gdw m⁻² for a *Spartina patens* community.

^dEstimated assuming 30 °C

^eEstimated using 0.43 gC gdw⁻¹

^fEstimated using 0.4 gC gdw⁻¹ and 900 gdw m⁻²

^gEstimated using 0.006 gN gdw⁻¹ root-rhizome tissue

^hAverage calculated from other studies listed for use in Goodwin Islands model

be the most dominant parameter and values calculated from the literature vary with methods, geographic locations, and conversion units and range 0.01-0.36 d⁻¹ (Table 6).

The dynamics of 37 different state variables can be represented by these four littoral zone habitat models (Figure 2) and there are a large number of habitat and ecosystem functions that can be investigated using the current models. But the models do not have state variables or process equations for several important ecosystem components. The physical models assume no advective or stochastic processes. The elevation (deposition and accretion) and biogeochemistry (TPOC, DOC, TDIN) of the sediment environment are essential components necessary to completely connect water column processes to sediment primary production in shallow and intertidal habitats. The dynamics of particulate and dissolved organic and inorganic phosphorus (POP, DOP, DIP), the processes regulating dissolved organic nitrogen (DON), and the macrophyte contribution to ecosystem DOC dynamics also have not been included in the current models. Currently there are four individual habitat models and an early goal of this study was to create one ecosystem model that includes all four of the habitats linked in model space and time. Because there are four individual models each model must have two boundary conditions for each water column constituent (appendix b). Channel boundary conditions were determined using the 1993 Virginia Water Quality reports (Curling and Neilson, 1994) and the boundary conditions for adjacent habitats for an individual model were established by calculating the annual average concentration for each constituent from the output of the adjacent model(s). The four models must be linked in model space and include sediment related processes for a more comprehensive picture of littoral zone functioning.

The output of only a few of these state variables have been validated in this summary. While one of the objectives of this modeling project was to organize data relevant to Chesapeake Bay littoral zone ecology, another was to identify information that

was lacking. Validation data are required for sediment microalgal production and biomass, the annual patterns of DOC in each of the littoral zone habitats, and the habitat scale horizontal exchange of water column materials among the habitats. Other information including the relationships between sediment microalgal production and the effects of macrophyte canopy shading, the role of sediment microalgae in vertical biogeochemical fluxes, and the determination of nutrient uptake rates of the various primary producers would be beneficial to further model development and implementation. New research and data are required on many of the same ecosystem components and processes that are missing from the models (see above).

These models are being used to investigate ecosystem structure, function, and change in the estuarine littoral zone. The models are used to assess material flux and generate estimates of primary production and nitrogen demand for the individual primary producers (phytoplankton, sediment microalgae, *Zostera marina*, *Spartina alterniflora*) and for the four primary habitats (Buzzelli Section 4). The models are being used to study management oriented environmental scenarios including the effects of altered vegetated subtidal and/or intertidal habitat size, the effects of increases in mean sea level (MSL), and the influence of increased nutrient loading at the offshore or terrestrial boundaries upon ecosystem primary production and water quality.

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appendix a. List of auxiliary equations for the four littoral zone habitat models of the Goodwin Islands National Estuarine Research Reserve. The formulations for diatoms and other plankton are similar. The formulations for labile and particulate organic carbon are also similar. Please refer to Wetzel and Neckles (1986) for formulations related to *Zostera marina* and epiphytic carbon production.

Diatom Gross Production (gC d⁻¹)

$$\text{Dia}_{\text{prod}} = \text{Dia}_{\text{hab}} \cdot \text{diaPmax} \cdot \text{DiaPTctrl} \cdot \text{DiaG}_{\text{lim}}$$

Diatom Photosynthesis Temperature Control (unitless)

$$\text{DiaPTctrl} = e^{(-\text{DiaPTI} \cdot (T_{\text{water}} - \text{DiaPTopt}))} \quad (\text{if } T_{\text{water}} \leq \text{DiaPTopt})$$

$$= e^{(-\text{DiaPTI} \cdot (\text{DiaPTopt} - T_{\text{water}}))} \quad (\text{if } T_{\text{water}} \geq \text{DiaPTopt})$$

Diatom Growth Limitation (unitless)

$$\text{DiaG}_{\text{lim}} = \text{MAX}(\text{DiaN}_{\text{lim}}, \text{DiaI}_{\text{lim}}) \quad (\text{If } \text{PAR}_u > 0.0)$$

Diatom Irradiance Control (unitless)

$$\text{DiaI}_{\text{lim}} = \frac{\text{PAR}_{\text{hab}}}{(\text{PAR}_{\text{hab}} + \text{DiaIK})}$$

Diatom Nitrogen Limitation Function (unitless)

$$\text{DiaN}_{\text{lim}} = \frac{\text{TDIN}_{\text{hab}}}{(\text{TDIN}_{\text{hab}} + \text{DiaKDIN})}$$

Diatom Respiration (gC d⁻¹)

$$\text{Dia}_{\text{resp}} = \text{Dia}_{\text{hab}} \cdot \text{DiaRTctrl}$$

Diatom Respiration Control with Temperature (d⁻¹)

$$\text{DiaRTctrl} = \text{BMRd} \cdot e^{(\text{KtBd} \cdot (T_{\text{water}} - \text{DiaRTopt}))}$$

Diatom Mortality (gC d⁻¹)

$$\text{Dia}_{\text{mort}} = \text{Dia}_{\text{hab}} \cdot \text{DiaMTctrl}$$

Diatom Mortality Control with Temperature (d⁻¹)

$$\text{DiaMTctrl} = \text{PPRd} \cdot e^{(\text{KtBd} \cdot (T_{\text{water}} - \text{DiaRTopt}))}$$

Diatom Exudation (gC d⁻¹)

$$\text{Dia}_{\text{exu}} = \text{Dia}_{\text{prod}} \cdot \text{DiaExuK}$$

Diatom Sedimentation (gC d⁻¹)

$$\text{Dia}_{\text{sed}} = \frac{\text{Dia}_{\text{hab}} \cdot \text{DiaSedK}}{h_{\text{hab}}}$$

Total POC Production (gC d⁻¹)

$$\text{TPOC}_{\text{prod}} = \text{PhytoPOCf} \cdot (\text{Dia}_{\text{mort}} + \text{OP}_{\text{mort}}) + \text{SM}_{\text{resus}}$$

Labile POC Production (gC d⁻¹)

$$\text{LPOC}_{\text{prod}} = \text{FLPOC} + \text{TPOC}_{\text{prod}}$$

Labile POC Hydrolysis (gC d⁻¹)

$$\text{LPOC}_{\text{hydrol}} = \text{LPOC}_{\text{hab}} * \text{KLC} * \text{HydrolTC}$$

$$\text{HydrolTC} = e^{(\text{KHydrol} * (\text{T}_{\text{water}} - \text{TrHydrol}))}$$

Labile POC Settling (gC d⁻¹)

$$\text{LPOC}_{\text{set}} = \frac{\text{LPOC}_{\text{hab}} * \text{StlV}_{\text{det}}}{h_{\text{hab}}}$$

Total DOC Production (gC d⁻¹)

$$\text{TDOC}_{\text{prod}} = (\text{LPOC}_{\text{hydrol}} + \text{RPOC}_{\text{hydrol}}) + (\text{Dia}_{\text{exu}} + \text{OP}_{\text{exu}})$$

Total DOC Remineralization (gC d⁻¹)

$$\text{DOC}_{\text{remin}} = \text{DOC}_{\text{hab}} * \text{KDC} * (1 - \text{FRDOC}) * \text{ReminTC}$$

$$\text{ReminTC} = e^{(\text{KRemin} * (\text{T}_{\text{water}} - \text{TrRemin}))}$$

Total DIN Production (mmoleN d⁻¹)

$$\text{TDIN}_{\text{prod}} = \text{DOC}_{\text{remin}} * \frac{1000}{\text{DOMCN} * 14}$$

Total DIN Uptake (mmoleN d⁻¹)

$$\text{TDIN}_{\text{uptake}} = \text{DiaN}_{\text{upt}} + \text{OPN}_{\text{upt}}$$

$$\text{TDIN}_{\text{VSTuptake}} = \text{DiaN}_{\text{upt}} + \text{OPN}_{\text{upt}} + \text{ZSHN}_{\text{upt}}$$

Total DIN Sediment Water Flux (mmoleN d⁻¹)

$$\text{TDIN}_{\text{sed}} = \text{TDIN}_{\text{flx_methavg}}$$

Sediment Microalgae Carbon Loss Through Grazing (gC m⁻² d⁻¹)

$$\text{SMC}_{\text{loss}} = (\text{SMMK} * \text{SMC}^2)$$

Sediment Microalgae Carbon Loss Through Resuspension (gC m⁻² d⁻¹)

$$\text{SMC}_{\text{res}} = \text{SMC} * \text{SMresK}$$

Zostera marina Carbon Translocation (gC m⁻² d⁻¹)

$$\text{ZC}_{\text{trans}} = \text{ZC}_{\text{pot}} - \text{ZSC}_{\text{net}} \quad (\text{If } \text{ZSCfb} < 1.0)$$

$$\text{ZC}_{\text{trans}} = \text{ZSC}_{\text{net}} \quad (\text{If } \text{ZSCfb} = 1.0)$$

Zostera marina shoot carbon biomass feedback function (ZSCfb; unitless)

$$\text{ZSCfb} = \frac{\text{ZSC} - \text{ZSClim}}{\text{ZSCmax} - \text{ZSClim}}$$

Zostera marina Shoot Nitrogen Uptake (gN m⁻² d⁻¹)

$$\text{ZSN}_{\text{uptake}} = \text{ZSN} * \text{ZSNmm}$$

Zostera marina Shoot Nitrogen Uptake ($gN\ gN^{-1}\ d^{-1}$)

$$ZSN_{mm} = ZSCNfb \cdot ZSC_{relgru} \cdot ZSVmN \cdot \left(\frac{TDIN_{hab}}{TDIN_{hab} + ZSKs} \right)$$

Zostera marina Shoot C:N Feedback Function (unitless)

$$ZSCNfb = \frac{ZSCN - ZSCNmin}{ZSCNmax - ZSCNmin} \quad \left(\text{where } ZSCN = \frac{ZSC}{ZSN} \right)$$

Zostera marina Shoot Relative Growth (unitless)

$$ZSC_{relgru} = \frac{ZS_{shoot}}{ZPT}$$

Zostera marina Nitrogen Translocation from Root-Rhizomes to Shoots ($gN\ m^{-2}\ d^{-1}$)

$$ZN_{trans} = (ZSN_{demand} - ZSN_{uptake}) \cdot (ZSCNfb) \cdot (1 - ZRRCNfb)$$

Zostera marina Shoot Nitrogen Demand ($gN\ m^{-2}\ d^{-1}$)

$$ZSN_{demand} = \frac{ZSC_{net}}{ZSCN_{opt}}$$

Zostera marina Shoot Nitrogen Loss ($gN\ m^{-2}\ d^{-1}$)

$$ZSN_{loss} = \frac{ZSC}{ZSCN}$$

Zostera marina root-rhizome respiration ($ZRRC_{resp};\ gC\ m^{-2}\ d^{-1}$)

$$ZRRC_{resp} = ZRRC \cdot ZRRRT$$

Zostera marina root-rhizome respiration temperature control ($ZRRRT; d^{-1}$)

$$ZRRRT = ZRRR@20 \cdot ZRRRK^{(T_{root} - ZRRRT_{ref})}$$

Spartina alterniflora Below Ground Spring Pulse (d^{-1})

$$SBGsp = SSPmax \cdot e^{-SSP1 \cdot (JD - SSPJD)^2} \quad (\text{If } JD \leq SSPJD)$$

$$SBGsp = SSPmax \cdot e^{-SSP2 \cdot (SSPJD - JD)^2} \quad (\text{If } JD > SSPJD)$$

appendix b. Complete list of parameters, boundary conditions, and constants for the four littoral zone habitat models of the Goodwin Islands National Estuarine Research Reserve.

Temporal and Spatial Considerations

JD	Julian Day	d	
dt	Integration Stepsize (Subtidal)	d	0.03125
	Integration Stepsize (Intertidal)	d	0.0078125
modhrs	Continuous Model Time in Hours	h	
thours	Daily Model Time in Hours	h	
Area	Habitat and Ecosystem Areas	m ²	

Habitat Depth Parameters

Abbreviation	Description	Units	Value
MSL	Mean Sea Level	m	0.00
hfilm	Intertidal Permanent Water Film Thickness	m	0.01
zNVST	NonVeg Subtidal Reference Elevation	m	-1.88
zVST	VegSubtidal Reference Elevation	m	-0.88
zNVIT	NonVeg Intertidal Reference Elevation	m	-0.36
zVIT	Veg Intertidal Reference Elevation	m	-0.00
Area _{NVST}	NonVeg Subtidal Wetted Area	m ²	420e04
Area _{VST}	Veg Subtidal Wetted Area	m ²	120e04
Area _{NVIT}	NonVeg Intertidal Maximum Wetted Area	m ²	100e04
Area _{VIT}	Veg Intertidal Maximum Wetted Area	m ²	85e04

Irradiance Attenuation Parameters

Abbreviation	Description	Units	Value
K _{water}	PAR attenuation constant for Water	m ⁻¹	0.04
POC _{atn}	PAR attenuation due to Suspended Detritus	m ² gC ⁻¹	0.14
DOC _{atn}	PAR attenuation due to water column DOC	m ² gC ⁻¹	0.14
Chl _{atn}	PAR attenuation due to water column Chla	m ² mgChla ⁻¹	0.0138
a _{Zm}	Vertical PAR attenuation due to <i>Zostera marina</i> biomass	m ² gC ⁻¹	0.002
a _{Sa}	Vertical PAR attenuation due to <i>Spartina alterniflora</i> biomass	m ² gC ⁻¹	0.002

Boundary Concentration Parameters

Abbreviation	Description	Units	Value
ChanDiaC	Channel Diatom C Concentration	gC m ⁻³	variable

ChanOPC	Channel Other Plankton C Concentration	gC m ⁻³	variable
ChanDOC	Channel DOC Concentration	gC m ⁻³	0.7
ChanLPOC	Channel Labile POC Concentration	gC m ⁻³	2.75
ChanRPOC	Channel Refractory POC Concentration	gC m ⁻³	2.25
ChanTDIN	Channel Total DIN Concentration	μM	20.0
NVSTDiaC	NonVeg Subtidal Diatom C Concentration	gC m ⁻³	0.165
NVSTOPC	NonVeg Subtidal Other Plankton C Concentration	gC m ⁻³	0.330
NVSTLPOC	NonVeg Subtidal Labile POC Concentration	gC m ⁻³	2.75
NVSTRPOC	NonVeg Subtidal Refractory POC Concentration	gC m ⁻³	2.25
NVSTDOC	NonVeg Subtidal DOC Concentration	gC m ⁻³	0.7
NVSTDIN	NonVeg Subtidal DIN Concentration	μM	10.0
VSTDiaC	Veg Subtidal Diatom C Concentration	gC m ⁻³	0.165
VSTOPC	Veg Subtidal Other Plankton C Concentration	gC m ⁻³	0.330
VSTLPOC	Veg Subtidal Labile POC Concentration	gC m ⁻³	2.75
VSTRPOC	Veg Subtidal Refractory POC Concentration	gC m ⁻³	2.25
VSTDOC	Veg Subtidal DOC Concentration	gC m ⁻³	0.7
VSTDIN	Veg Subtidal DIN Concentration	μM	10.0
NVITDiaC	NonVeg Intertidal Diatom C Concentration	gC m ⁻³	0.165
NVITOPC	NonVeg Intertidal Other Plankton C Concentration	gC m ⁻³	0.330
NVITLPOC	NonVeg Intertidal Labile POC Concentration	gC m ⁻³	2.75
NVITRPOC	NonVeg Intertidal Refractory POC Concentration	gC m ⁻³	2.25
NVITDOC	NonVeg Intertidal DOC Concentration	gC m ⁻³	3.5
NVITDIN	NonVeg Intertidal DIN Concentration	μM	5.0
VITDiaC	Veg Intertidal Diatom C Concentration	gC m ⁻³	0.165
VITOPC	Veg Intertidal Other Plankton C Concentration	gC m ⁻³	0.330
VITLPOC	Veg Intertidal Labile POC Concentration	gC m ⁻³	2.75

VITRPOC	Veg Intertidal Refractory POC Concentration	gC m^{-3}	2.25
VITDOC	Veg Intertidal DOC Concentration	gC m^{-3}	3.5
VITDIN	Veg Intertidal DIN Concentration	μM	5.0
Global Algal Rate Parameters			
Abbreviation	Description	Units	Value
OPttlPhyto	Other Plankton:Total Phytoplankton	unitless	0.67
CChla	Diatom and OP Carbon:Chla	unitless	50.0
PPOCf	Fraction of Phyto Mort to POC	unitless	0.80
BMRd	Diatom Basal Metabolic Rate	d^{-1}	0.015
KtBd	Constant for Diatom Respiration Temperature Function	$^{\circ}\text{C}^{-1}$	0.069
DIAExK	Diatom Exudation Constant	unitless	0.30
DIAPT1	Diatom Photosynthesis Temperature Coefficient 1	unitless	0.004
DIAPT2	Diatom Photosynthesis Temperature Coefficient 2	unitless	0.006
DIASdK	Diatom Sedimentation Coefficient	m d^{-1}	0.25
DIACN	Diatom C:N Ratio (weight)	unitless	5.7
DIAIK	Diatom Half-Saturation Constant for Photosynthesis	$\mu\text{E m}^{-2} \text{s}^{-1}$	140
DIAKsN	Diatom Half-Saturation Constant for Nitrogen Uptake	μM	10.0
DIAPmax	Diatom Maximum Photosynthetic Rate	d^{-1}	0.50
DIAPTopt	Reference Temperature for Diatom Photosynthesis	$^{\circ}\text{C}$	20.0
DIARTopt	Reference Temperature for Diatom Respiration	$^{\circ}\text{C}$	20.0
PRRd	Predation Rate on Diatoms (Mortality)	d^{-1}	0.15
BMRop	Other Plankton Basal Metabolic Rate	d^{-1}	0.015
KTBoP	Constant for OP Respiration Temperature Function	$^{\circ}\text{C}^{-1}$	0.069
OPExK	Other Plankton Exudation Constant	unitless	0.30
OPSdK	Other Plankton Sedimentation Constant	m d^{-1}	0.10
OPCN	Other Plankton C:N (weight)	unitless	5.7
OPIK	Other Plankton Half-Saturation Constant for Photosynthesis	$\mu\text{E m}^{-2} \text{s}^{-1}$	140
OPKDin	Other Plankton Half-Saturation Constant for Nitrogen Uptake	μM	10.0
OPPmax	Other Plankton Maximum Photosynthetic Rate	d^{-1}	0.50

OPPT _{opt}	Reference Temperature for Other Plankton Photosynthesis	°C	25.0
OPRT _{opt}	Reference Temperature for Other Plankton Respiration	°C	20.0
OPPT1	Other Plankton Photosynthesis Temperature Coefficient 1	unitless	0.008
OPPT2	Other Plankton Photosynthesis Temperature Coefficient 2	unitless	0.010
PRR _{op}	Predation Rate on Other Plankton	d ⁻¹	0.15
SMCN _{opt}	Sediment Microalgae optimal C:N	unitless	5.7
SMIK	Sediment Microalgae Half Saturation Constant for Photosynth.	μE m ⁻² s ⁻¹	100
SMP _{max}	Sediment Microalgae Maximum Photosynthetic Rate	d ⁻¹	0.576
BMR _{sm}	Sediment Microalgae Basal Respiration Rate	d ⁻¹	0.05
KtB _{sm}	Constant for Sediment Microalgae Respiration Temperature Function	°C ⁻¹	0.069
SMRT _{opt}	Reference Temperature for Sediment Microalgae Respiration	°C	20.0
SmMK	Sediment Microalgal Mortality Constant	m ² gC ⁻¹ d ⁻¹	0.045
SmJ _{Dm}	Sediment Microalgae Julian Day Mortality	day	45
SMResK	Sediment Microalgae Resuspension Constant	d ⁻¹	0.05
Global Kinetic Parameters			
Abbreviation	Description	Units	Value
StlV _{det}	Detritus Settling Velocity	m d ⁻¹	0.25
DOMCN	Dissolved OM C:N ratio	unitless	10.0
POMCN	Particulate OM C:N ratio	unitless	10.0
DOMCN	Dissolved OM C:N ratio	unitless	10.0
FLPOC	Labile POC Fraction	unitless	0.55
FRDOC	Refractory DOC Fraction	unitless	0.00*
FRPOC	Refractory POC Fraction	unitless	0.45
KDC	Constant for DOC Remineralization	d ⁻¹	0.01
KLC	Constant for LPOC Hydrolysis	d ⁻¹	0.075
KRC	Constant for RPOC Hydrolysis	d ⁻¹	0.005
Kh _{hydrol}	Constant for POC Hydrolysis. Temperature Function	°C ⁻¹	0.069
KRemin	Constant for DOC Remin. Temperature Function	°C ⁻¹	0.069
Tr _{Hydrol}	Reference Temperature for POC Hydrolysis	°C	20.0
TrRemin	Reference Temperature for DOC Remineralization	°C	20.0

<i>Zostera</i> Related Parameters			
Abbreviation	Description	Units	Value
ZIK	Half-Saturation Irradiance for <i>Zostera</i> photosynthesis	$\mu\text{E m}^{-2} \text{ s}^{-1}$	57.5
ZCpot	Potential Fraction of <i>Zostera</i> Shoot Production Translocated	unitless	0.25
ZIPOCdep	Potential Fraction of <i>Zostera</i> Shoot POC deposited	unitless	0.50
ZJDM	<i>Zostera</i> Shoot Fall JD Mortality	unitless	333
ZSFMK	<i>Zostera</i> Shoot Fall Mortality Constant	d^{-1}	0.0135
ZSmk1	<i>Zostera</i> Shoot Mortality Coefficient 1	unitless	0.0003
ZSmk2	<i>Zostera</i> Shoot Mortality Coefficient 1	unitless	0.0005
ZSmax	<i>Zostera</i> Shoot Maximum Biomass	gC m^{-2}	200
ZSlim	<i>Zostera</i> Shoot Density Limitation Concentration	gC m^{-2}	100
ZSCDW	<i>Zostera</i> Shoot Carbon Content	gC gdw^{-1}	0.40
ZSCNmax	<i>Zostera</i> Shoot Maximum C:N (weight)	unitless	22
ZSCNmin	<i>Zostera</i> Shoot Minimum C:N (weight)	unitless	12
ZSCNopt	<i>Zostera</i> Shoot Optimal C:N (weight)	unitless	16
ZSKsN	<i>Zostera</i> Shoot Half Saturation Constant for N Uptake	μM	10
ZSVmN	<i>Zostera</i> Shoot Maximum Nitrogen Uptake Rate	d^{-1}	0.021
ZRRmax	<i>Zostera</i> Root-rhizome Biomass Maximum	gC m^{-2}	200
ZRRlim	<i>Zostera</i> Root-rhizome Density Limitation Concentration	gC m^{-2}	100
ZRRCNmax	<i>Zostera</i> Root-rhizome Maximum C:N ratio (weight)	unitless	28
ZRRCNmin	<i>Zostera</i> Root-rhizome Minimum C:N ratio (weight)	unitless	15
ZRRCNopt	<i>Zostera</i> Root-rhizome Optimal C:N ratio (weight)	unitless	25
ZRRKsN	<i>Zostera</i> Root-rhizome Half Saturation Constant for N Uptake	μM	30
ZRRR@20	<i>Zostera</i> Root-rhizome Respiration Rate at 20 °C	d^{-1}	0.0005
ZRRRK	<i>Zostera</i> Root-rhizome Respiration Constant	unitless	1.25
ZRRTref	<i>Zostera</i> Root-rhizome Metabolic Reference Temperature	°C	20.0

ZRRVmN	<i>Zostera</i> Root-rhizome Maximum Nitrogen Uptake Rate	d ⁻¹	0.072
ZRRbk	<i>Zostera</i> Root-rhizome Bed Storage Constant	unitless	0.05
BMRZepi	<i>Zostera</i> Epiphyte Basal Metabolic Rate	d ⁻¹	0.045
KtBZepi	Constant for <i>Zostera</i> Epiphyte Respiration Temperature Function	°C ⁻¹	0.069
ZEpiGK	<i>Zostera</i> Epiphyte Grazing Constant	m ² gC ⁻¹ d ⁻¹	0.001
ZEpiRTopt	Reference Temperature for <i>Zostera</i> Epiphyte Respiration	°C	20.0

Spartina Related Parameters

Abbreviation	Description	Units	Value
SCgdw	<i>Spartina</i> Shoot Carbon Content	gC gdw ⁻¹	0.40
SCTpot	<i>Spartina</i> Maximum Fractional Downward Carbon Translocation	unitless	0.75
SfPOCdep	Fraction of <i>Spartina</i> Shoot Carbon to Sediment POC Pool	unitless	0.90
SIK	Half Saturation Constant for <i>Spartina</i> Photosynthesis	μE m ⁻² s ⁻¹	265
SPmax	<i>Spartina</i> Maximum Photosynthetic Rate	d ⁻¹	0.15
SSC _{bmort}	<i>Spartina</i> Shoot Basal Mortality	d ⁻¹	0.00375
SSCNmax	<i>Spartina</i> Shoot Maximum C:N ratio (weight)	unitless	30
SSCNmin	<i>Spartina</i> Shoot Minimum C:N ratio (weight)	unitless	20
SSCNopt	<i>Spartina</i> Shoot Optimum C:N ratio (weight)	unitless	
SSR@20	<i>Spartina</i> Shoot Respiration at 20 °C	d ⁻¹	0.01
SSRK	<i>Spartina</i> Shoot Respiration Constant	unitless	1.07
SSRTref	<i>Spartina</i> Shoot Metabolic Reference Temperature	°C	20.0
SSPK1	<i>Spartina</i> Shoot Spring Pulse Constant 1	unitless	0.025
SSPK2	<i>Spartina</i> Shoot Spring Pulse Constant 2	unitless	0.025
SSPJD	<i>Spartina</i> Shoot Spring Pulse Julian Day	unitless	115
SSprmax	<i>Spartina</i> Shoot Spring Pulse Maximum	d ⁻¹	0.01
SSJDM	<i>Spartina</i> Shoot Mortality Onset Julian Day	unitless	190
SSTK1	<i>Spartina</i> Shoot Photosynthesis Temperature Constant 1	unitless	0.005

SSTK2	<i>Spartina</i> Shoot Photosynthesis Temperature Constant 2	unitless	0.002
SPTopt	<i>Spartina</i> Shoot Photosynthesis Temperature Control	°C	20
SRRCmax	<i>Spartina</i> Root-Rhizome Maximum Biomass	gC m ⁻²	1000
SRRCmin	<i>Spartina</i> Root-Rhizome Minimum Biomass	gC m ⁻²	500
SRRKsN	Half Saturation Constant for N Uptake by <i>Spartina</i> Root-Rhizomes	μM	100
SRRmK	<i>Spartina</i> Root-Rhizome Loss Constant	unitless	1.25
SRRM@20	<i>Spartina</i> Root-Rhizome Loss Rate at 20 °C	d ⁻¹	0.0006
SRRCNmax	<i>Spartina</i> Root-Rhizome Maximum C:N ratio (weight)	unitless	300
SRRCNmin	<i>Spartina</i> Root-Rhizome Minimum C:N ratio (weight)	unitless	80
SRRCNopt	<i>Spartina</i> Root-Rhizome Optimal C:N ratio (weight)	unitless	200
SRRR@20	<i>Spartina</i> Root-Rhizome Respiration Rate at 20 °C	d ⁻¹	0.0006
SRRRK	<i>Spartina</i> Root-Rhizome Respiration Constant	unitless	1.25
SRRTref	<i>Spartina</i> Root-Rhizome Metabolic Reference Temperature	°C	20.0
SRRbk	<i>Spartina</i> Root-Rhizome Bed Storage Constant	unitless	0.075
SRRVmN	<i>Spartina</i> Root-Rhizome Maximum Nitrogen Uptake Rate	d ⁻¹	0.134

Section 4

USE OF ECOSYSTEM MODELS TO INVESTIGATE ANNUAL PRIMARY
PRODUCTION AND MATERIAL EXCHANGE IN THE CHESAPEAKE BAY
LITTORAL ZONE

*To be submitted to Estuarine and Coastal Shelf Science

ABSTRACT

The estuarine littoral zone includes seagrass and marsh habitats situated between terrestrial and offshore boundaries. Studies that address the ecological dynamics within the littoral zone are necessary to better understand the interactions between the fringing environments and the watershed. This study investigated ecosystem function by utilizing a series of four simulation models of littoral zone habitats of the Goodwin Islands National Estuarine Research Reserve (NERR) to estimate annual primary productivity and material exchange. Of the total annual ecosystem net primary production, phytoplankton were 15.8%, sediment microalgae were 34.3%, *Zostera marina* community was 14.9%, and *Spartina alterniflora* was 35%. The nonvegetated subtidal and vegetated intertidal habitats accounted for 28% and 43% of total annual ecosystem production, respectively. The nonvegetated subtidal habitat is a major source of phytoplankton, and therefore, DOC and DIN to the other three habitats. The seagrass meadow is also a source of phytoplankton but is a sink for POC and plays a significant role in ecosystem biogeochemical cycling. The two intertidal habitats show net annual imports of all water column constituents. These models are being used to investigate relationships between water quality and seagrass community dynamics and the potential effects altered size and composition of habitats have upon ecosystem function.

INTRODUCTION

The estuarine littoral zone is comprised of a mosaic of different habitat types that are interconnected by the dynamic exchange of primary production, particulate and dissolved substances, and faunal populations (Correll et al., 1992; Childers et al., 1993; Kneib and Wagner, 1994; Rozas, 1995). A number of coastal studies have focused upon subsystem processes within coastal marsh and shallow nearshore ecosystems (Wolaver et al., 1983; Stevenson et al., 1988; Dame et al., 1991; Correll et al., 1992; Vorosmarty and Loder, 1994). These studies are important because they quantify material production and exchange in fringing habitats that are situated between channel and upland environments. Although biogeochemical processes in the fringing environments can be distinct from those of the adjacent channel, the two estuarine zones are linked on daily, seasonal, and annual time scales (Malone et al., 1986; Kuo and Park, 1995). Watershed factors such as riverine flow and nutrient runoff can influence the annual patterns of production and nutrient cycling in the estuarine littoral zone (Correll et al., 1992). In order to assess the function of the littoral zone in coastal landscape dynamics it is necessary to gain an understanding of the processes that occur within these fringing estuarine environments.

Process oriented simulation modeling of ecosystems offers a unique opportunity to organize available information, identify missing data, and analyze the dynamics of various ecosystem components (Christian and Wetzel, 1991). Dynamic simulation models can be used to integrate ecological processes over various combinations of spatial and temporal scales in order to assess the overall properties of ecosystems (Childers et al., 1993). Simulations performed under different combinations of driving factors can be used in ecosystem hindcasting and/or forecasting (Costanza et al., 1990; Cerco and Cole, 1993; Cerco, 1995). Geographic information systems (GIS) can be coupled with process models both to provide a source of spatially referenced input and as an effective method to visualize model output (Costanza et al., 1990; Lee et al., 1992). Simulation models can be used to

link field and geographic research methods in the investigation of coastal landscape dynamics (Lee et al., 1992) and can be used to generate new hypotheses and research objectives (Christian and Wetzel, 1991).

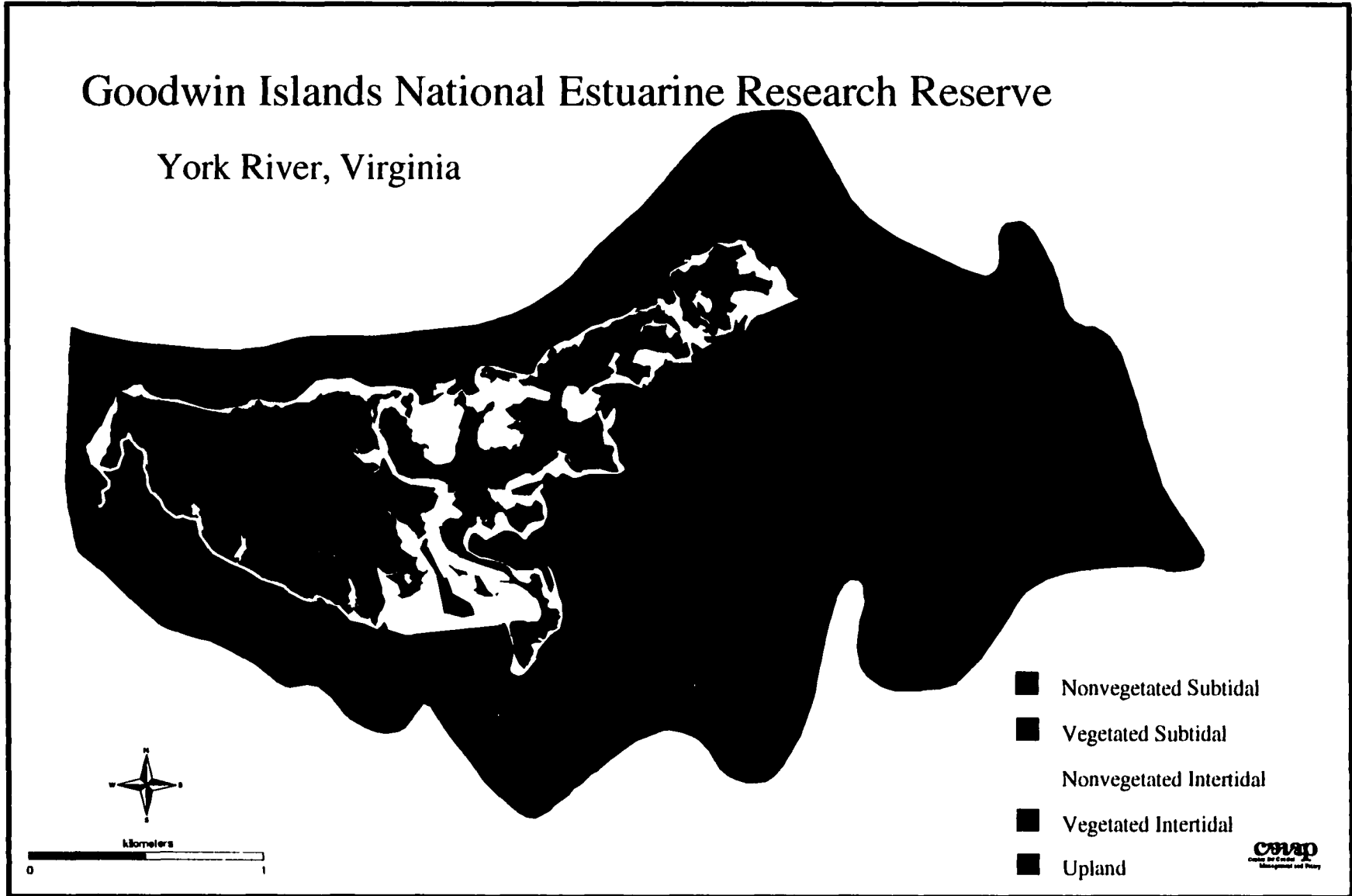
The primary objective of this study was to utilize a series of four individual simulation models to assess habitat and ecosystem function by providing estimates of annual primary production and material fluxes in the Chesapeake Bay littoral zone. The four models were based upon four primary littoral zone habitats identified for the Goodwin Islands National Estuarine Research Reserve (NERR) in lower Chesapeake Bay, Virginia (Buzzelli Sections 2 and 3). These models have been developed as research tools to provide an integrative framework with which to analyze estuarine ecosystems, to organize information and identify missing data, and to investigate the emergent ecological properties of the Goodwin Islands NERR.

METHODS

The Goodwin Islands NERR is located in the lower York River estuary (37° 12' 46'' N, 76° 23' 46'' W). The general ecological characteristics of this littoral zone ecosystem have been described in a previous section of this dissertation (Buzzelli Section 2). The littoral zone of the Goodwin Islands NERR was defined as the area between the -2.36 m depth (mean sea level) and the salt bush community located near mean higher high water (about +1.5 m). The littoral zone was divided into four primary habitats between offshore channel environments and forested upland boundaries and includes nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal marsh habitats (VIT; Fig. 1).

Conceptual and simulation models were derived for each habitat that include phytoplankton, sediment microalgae, and water column particulate and dissolved organic carbon and dissolved inorganic nitrogen (Fig. 2; Buzzelli Section 3). The principal forcing

Figure 1. Habitat map for the Goodwin Islands National Estuarine Research Reserve (NERR), York River, Virginia. This map was generated using a geographic information system of the NERR.



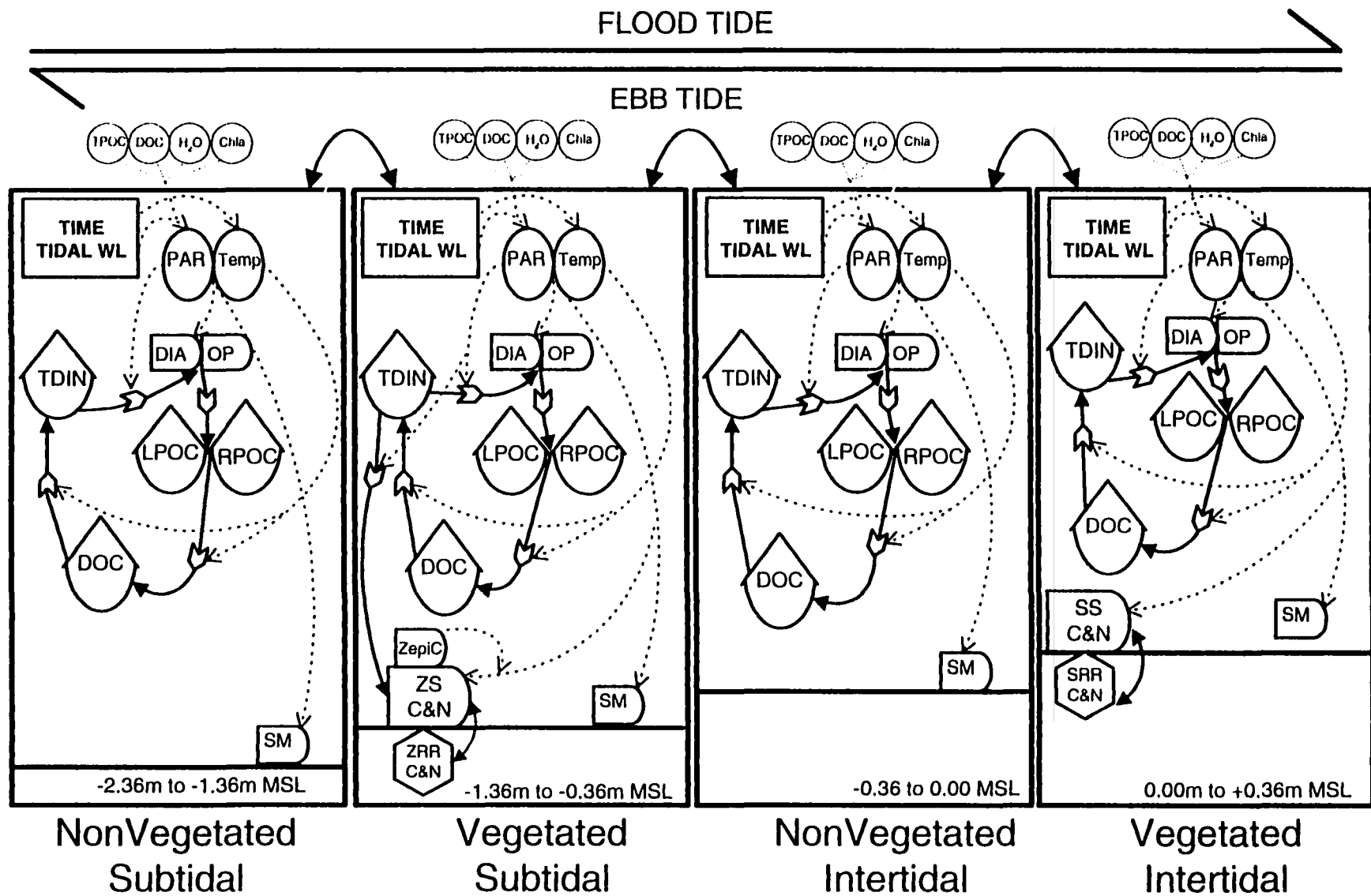
variables are tidal water level, solar insolation, and temperature. The vegetated subtidal and intertidal models contain carbon and nitrogen state variables for *Zostera marina* and *Spartina alterniflora*, respectively. Table 1 provides a list of the state variable abbreviations, definitions, and units. The habitats are connected by the volume exchange of suspended materials due to tidal forces (Fig. 2). Habitat volume is calculated from the habitat wetted area and depth. Wetted area (m^2) is constant in the two subtidal habitat models but the intertidal inundation is calculated using a hypsometric curve (Childers et al., 1993). Water column state variables are influenced by production, respiration, loss due to biogeochemical cycling, sedimentation and settling, and horizontal exchange with the adjacent habitats (Buzzelli Section 3). Sediment microalgal biomass changes with production, respiration, grazing, and resuspension. Subtidal and intertidal habitat sizes are constant for sediment microalgae although they are limited by light attenuation from changes in depth of the overlying water column and seasonal changes in macrophyte biomass (vegetated habitat models only; Buzzelli Section 3). Macrophyte carbon production is balanced by respiration, loss, and translocation while nitrogen is absorbed through the shoots and root-rhizomes (*Zostera marina*) or root-rhizomes only (*Spartina alterniflora*) and distributed within the plant to meet nitrogen growth requirements. The formulations for rate processes, tidal functions and horizontal exchanges, and model parameters have been described in the previous section of this dissertation (Buzzelli Section 3).

The nitrogen demand of each phototroph was calculated using the net carbon production rate and the optimal C:N ratio. The nitrogen uptake was calculated for the phytoplankton and the macrophytes, *Zostera marina* (shoots and root-rhizomes) and *Spartina alterniflora* (root-rhizomes) based upon the assumptions and parameters associated with Michaelis-Menten kinetics (Buzzelli Section 3). There are both carbon and nitrogen

Table 1. List of state variables for habitat models. Each habitat model includes the first 7 state variables listed. In addition to the basic seven the vegetated subtidal habitat model (VST) includes those related to *Zostera marina* while the vegetated intertidal habitat model (VIT) has those related to *Spartina alterniflora*. See Buzzelli Chapter 2 for state variable differential equations and complete mathematical descriptions.

ABBREV.	DESCRIPTION	UNITS
DIA	Diatom Carbon Mass	gC
OP	Other Plankton Carbon Mass	gC
LPOC	Labile Particulate Organic Carbon	gC
RPOC	Refractory Particulate Organic Carbon	gC
DOC	Dissolved Organic Carbon	gC
TDIN	Total Dissolved Inorganic Nitrogen	μM
SM	Sediment Microalgae	gC m^{-2}
ZSC	<i>Zostera marina</i> Shoot Carbon	gC m^{-2}
ZSN	<i>Zostera marina</i> Shoot Nitrogen	gN m^{-2}
ZRRC	<i>Zostera marina</i> Root-Rhizome Carbon	gC m^{-2}
ZRRN	<i>Zostera marina</i> Root-Rhizome Nitrogen	gN m^{-2}
ZepiC	<i>Zostera marina</i> Epiphytic Biomass	gC m^{-2}
SSC	<i>Spartina alterniflora</i> Shoot Carbon	gC m^{-2}
SSN	<i>Spartina alterniflora</i> Shoot Nitrogen	gN m^{-2}
SRRC	<i>Spartina alterniflora</i> Root-Rhizome Carbon	gC m^{-2}
SRRN	<i>Spartina alterniflora</i> Root-Rhizome Nitrogen	gN m^{-2}

Figure 2. Conceptual diagram for the four habitat simulation models of the Goodwin Islands NERR littoral zone. Each model is driven by tidal water level, insolation (PAR), and temperature and includes phytoplankton (DIA and OP), labile and refractory particulate organic carbon (LPOC and RPOC), dissolved organic carbon (DOC), sediment microalgae (SM), and total dissolved inorganic nitrogen (TDIN). The vegetated subtidal and intertidal habitat models also have carbon and nitrogen state variables related to *Zostera marina* and *Spartina alterniflora*, respectively.



state variables for macrophytes because they can internally translocate and recycle these elements. There are no formulations to represent nitrogen uptake by sediment microalgae although dissolved inorganic nitrogen is exchanged vertically within each habitat model based upon empirical observations (Buzzelli Section 3).

The results presented here are integrated annual rates that were derived from integrated daily rates. The annual rates of net primary productivity and nitrogen demand and uptake of each model phototroph were calculated along with the annual net carbon production and nitrogen demand of each of the four primary habitats. Annual primary productivity rates predicted using the model were compared to estimates derived from the literature. Both individual boundary and net exchanges of phytoplankton, particulate and dissolved organic carbon (POC and DOC), and dissolved inorganic nitrogen (DIN) were estimated for each habitat annually (see Buzzelli Section 3 for an explanation of model boundary processes). The productivity and flux characteristics of the four habitats were compared to identify material sources and sinks within the ecosystem. The annual net carbon production and suspended material budgets for the entire Goodwin Islands NERR were then calculated using the summed process estimates for each habitat. A geographic information system (GIS) of the Goodwin Islands NERR is in development to provide a framework upon which to base longer term studies of ecosystem patterns (Fig. 1).

RESULTS

Annual production by the diatom and other plankton state variables of the Goodwin Islands NERR habitat models was estimated at 66.0 gC m^{-2} (Table 2). The nonvegetated and vegetated subtidal areas were added to the average inundated area of each of the two intertidal habitats in order to calculate the total ecosystem size for phytoplankton production (671 m^2). Annual phytoplankton production was $442.7 \times 10^6 \text{ gC}$ which comprised

15.8% of the total annual production in the Goodwin Islands NERR. Sediment microalgae accounted for approximately 34% of the annual ecosystem productivity but annual net areal productivity rates ($\text{gC m}^{-2} \text{yr}^{-1}$) of sediment microalgae varied among the four habitats.

The nonvegetated intertidal (NVIT) habitat model predicted the highest rate at $169.0 \text{ gC m}^{-2} \text{yr}^{-1}$, followed by the intertidal marsh (VIT) at $162.5 \text{ gC m}^{-2} \text{yr}^{-1}$, the nonvegetated subtidal (VST) at $127.6 \text{ gC m}^{-2} \text{yr}^{-1}$, and the seagrass meadow habitat (VST) had the lowest at $101.2 \text{ gC m}^{-2} \text{yr}^{-1}$ (Table 2). The NVST habitat produced $535.9 \times 10^6 \text{ gC}$ which accounted for 19.1% of the total for the littoral zone of the Goodwin Islands NERR. The VST, NVIT, and VIT habitats contributed 4.3%, 6.0%, and 4.9% of the total annual primary production of the ecosystem, respectively (Table 2).

Zostera marina community production includes shoots, attached epiphytes, and the root-rhizomes (Buzzelli Section 3). *Zostera marina* epiphytes and root-rhizomes had a similar rate of annual primary productivity at approximately $55 \text{ gC m}^{-2} \text{yr}^{-1}$ (Table 2). These two state variables made up 4.6% of total ecosystem production. The shoots of *Zostera marina* had a net annual rate of $241.3 \text{ gC m}^{-2} \text{yr}^{-1}$ and accounted for about 10% of total ecosystem production. The *Zostera marina* community of the Goodwin Islands NERR produced approximately $421.7 \times 10^6 \text{ gC yr}^{-1}$ which was 15% of the total (Table 2). The shoots of *Spartina alterniflora* had the greatest annual net productivity rate of any of the model phototrophs at $830.8 \text{ gC m}^{-2} \text{yr}^{-1}$ while the root-rhizome net productivity rate was $319.7 \text{ gC m}^{-2} \text{yr}^{-1}$ (Table 2). Over the 85 hectares of the intertidal marsh habitat *Spartina alterniflora* shoots and root-rhizomes produced $977.9 \times 10^6 \text{ gC yr}^{-1}$ and accounted for 34.9% of the total ecosystem production predicted by the four habitat models.

Table 2. Estimates of annual net production and contribution to ecosystem production in the littoral zone of the Goodwin Islands NERR using the four habitat models. Phytoplankton productivity was summed over all 4 habitats and intertidal habitat size used in this summation is the average areal inundation during model simulation time (m²). The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT).

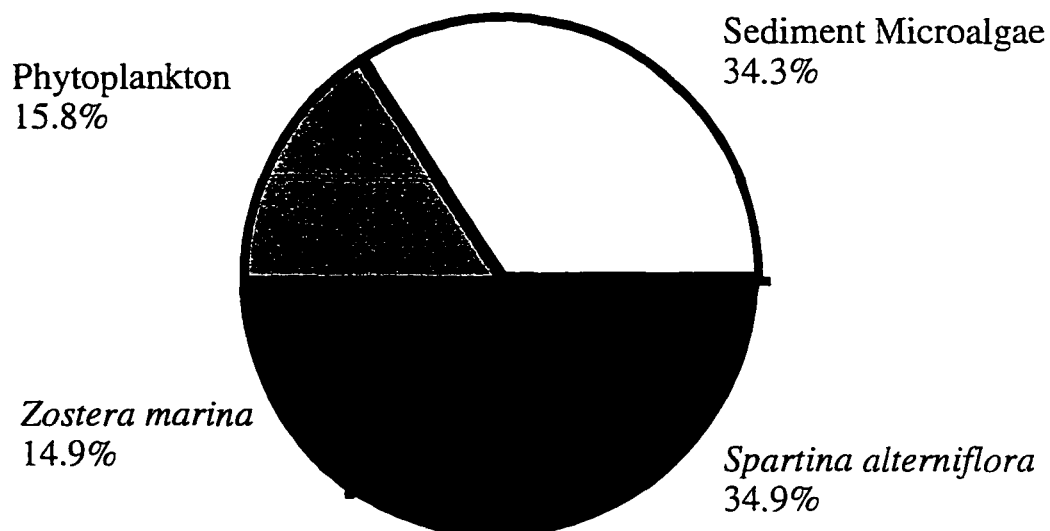
Photoautotrophic Component	Annual Net Production gC m ⁻² yr ⁻¹	Habitat Size 10 ⁴ m ⁻²	Annual Net Production 10 ⁶ gC yr ⁻¹	Percent of Total Ecosystem %
Phytoplankton	66.0	671	442.7	15.8
Sed. Microalgae				
NVST	127.6	420	535.9	19.1
VST	101.2	120	121.4	4.3
NVIT	169.0	100	169.0	6.0
VIT	162.5	85	138.1	4.9
<i>Zostera marina</i>				
Epiphytes	55.9	120	67.1	2.3
Shoot	241.3	120	289.6	10.3
RR	54.2	120	65.0	2.3
<i>Spartina alterniflora</i>				
Shoot	830.8	85	706.2	25.2
RR	319.7	85	271.7	9.7
TOTAL			2806.7	99.9

The fractions of each phototroph's contribution to total ecosystem production of the Goodwin Islands NERR were plotted for comparison to the results from a study of another Atlantic coastal marsh-estuarine ecosystem, the North Inlet, South Carolina (Pinckney and Zingmark, 1993). The North Inlet study utilized photophysiological models of sediment microalgal production to integrate annual primary production and then estimated the contribution by the other phototrophs using data assembled from other studies (Pinckney and Zingmark, 1993). Phytoplankton accounted for 15.8% of total ecosystem production in the Goodwin Islands NERR compared to 20.8% in the North Inlet ecosystem (Fig. 3). Sediment microalgal contribution among the two ecosystems compared favorably with approximately 30% of the annual net production by sediment microalgae (Fig. 3). *Spartina alterniflora* productivity was responsible for approximately 35% of total production among the two ecosystems while the productivity of *Zostera marina* in the Goodwin Islands NERR (14.9%) was similar to that contributed by macroalgae in the North Inlet ecosystem (13.5%).

Table 3 summarizes the annual nitrogen demand and uptake by each of the phototrophic components of the Goodwin Islands NERR habitat models. Based upon an annual production rate of $66.0 \text{ gC m}^{-2} \text{ yr}^{-1}$ and the Redfield C:N weight ratio (5.7), the annual phytoplankton nitrogen requirement was $11.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ (Table 3). Annual phytoplankton nitrogen uptake estimated by the models was $15.7 \text{ gN m}^{-2} \text{ yr}^{-1}$. Using the areal production rates provided in Table 3 and a C:N of 5.7 sediment microalgae required 22.4, 13.8, 29.6, and $28.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ in the NVST, VST, NVIT, and VIT habitats, respectively (Table 3). The annual nitrogen requirement for *Zostera marina* shoots and root-rhizomes was $16.0 \text{ gN m}^{-2} \text{ yr}^{-1}$ while the actual nitrogen uptake was $5.95 \text{ gN m}^{-2} \text{ yr}^{-1}$. The annual nitrogen requirement of *Spartina alterniflora* was $27.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ while

Figure 3. Comparison of the contributions of various phototrophs to net ecosystem primary production between the (A) Goodwin Islands NERR, and the (B) North Inlet, South Carolina ecosystem (from Pinckney and Zingmark, 1993).

(A) Goodwin Islands NERR Ecosystem Primary Production



(B) North Inlet, SC Ecosystem Primary Production (Pinckney and Zingmark 1993)

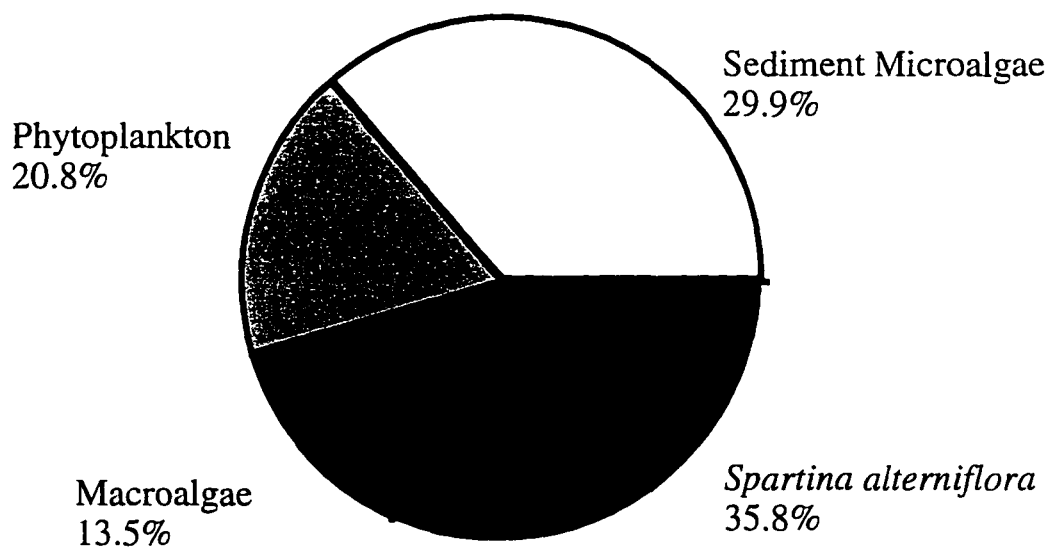


Table 3. Estimates of annual nitrogen demand and uptake for estuarine phototrophs using the Goodwin Islands habitat models. Demand is calculated using the net carbon production and the optimal C:N ratio. Uptake is calculated using a Michaelis-Menten relationship based upon external nitrogen concentration, a half-saturation value, and the maximum uptake rate. Phytoplankton nitrogen processes were summed over the four separate habitat models. The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT).

Photoautotrophic Component	Annual Nitrogen Demand gN m ⁻² yr ⁻¹	Annual Nitrogen Uptake gN m ⁻² yr ⁻¹
Phytoplankton	11.5	15.7
Sediment Microalgae		
NVST	22.4	na
VST	17.8	na
NVIT	29.6	na
VIT	28.5	na
<i>Zostera marina</i>		
shoots	15.1	2.09
root-rhizomes	<u>0.89</u>	<u>3.86</u>
total	16.0	5.95
<i>Spartina alterniflora</i>		
shoots	26.0	na
root-rhizomes	<u>1.53</u>	<u>11.5</u>
total	27.5	11.5

the root-rhizome uptake rate was $11.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ (Table 3).

The annual carbon production and nitrogen demand of each of the phototrophs present in each of the habitat models were calculated in order to compare the four different littoral zone habitats based on current size and composition (Table 4). The nonvegetated subtidal habitat model (NVST) predicted $740 \times 10^6 \text{ gC yr}^{-1}$ which was 28.6% of the total ecosystem annual net primary production. The NVST habitat required $130 \times 10^6 \text{ gN}$ for this rate of primary production and the nitrogen demand was over 50% of that of the entire ecosystem (Table 4). The vegetated subtidal habitat model (VST) generated an annual net carbon production of $562 \times 10^6 \text{ gC}$ which represented 21.7% of total ecosystem production. The VST habitat required $440 \times 10^6 \text{ gN}$ to sustain this level of production and the VST nitrogen requirement was 17.4% of the total (Table 4). The nonvegetated intertidal habitat model predicted $170 \times 10^6 \text{ gC}$ of annual net production and was 6.6% of the ecosystem total. Approximately $30 \times 10^6 \text{ gN}$ or 11.9% of the ecosystem nitrogen demand was required to sustain this level of production in the NVIT habitat. The vegetated intertidal marsh habitat model (VIT) predicted the highest annual net carbon production among the four habitats at $1116 \times 10^6 \text{ gC}$ which comprised 43.1% of the total. The nitrogen required to sustain this net productivity rate was $47 \times 10^6 \text{ gN}$ which made up the final 19.0% of the total ecosystem nitrogen demand (Table 4).

The four habitat models were used to estimate the annual net material fluxes for each habitat and the whole littoral zone of the Goodwin Islands NERR (Table 5). The water column constituents summarized include total phytoplankton (gC yr^{-1}), TPOC (gC yr^{-1}), DOC (gC yr^{-1}), and TDIN (gN yr^{-1}). Net import is designated as a negative flux while net export is shown as a positive flux. The nonvegetated subtidal habitat model

Table 4. Estimates of net annual carbon production and nitrogen demand of each of the four littoral zone habitats of the Goodwin Islands NERR using the four habitat simulation models. The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT). Each habitat model includes diatoms, other plankton, and sediment microalgae. In addition to algae the vegetated subtidal and intertidal habitat models include the net shoot and root-rhizome production by *Zostera marina* and *Spartina alterniflora*, respectively.

Habitat	Size (ha)	Percent of Total Size	Annual C Production gC	Percent of Total C Production	Annual N Demand gN	Percent of Total N Demand
NVST	420	51.9%	740 x 10 ⁶	28.6%	130 x 10 ⁶	51.7%
VST	120	18.5%	562 x 10 ⁶	21.7%	44 x 10 ⁶	17.4%
NVIT	100	12.3%	170 x 10 ⁶	6.6%	30 x 10 ⁶	11.9%
VIT	85	11.1%	1116 x 10 ⁶	43.1%	47 x 10 ⁶	19.0%

Table 5. Estimates of annual material exchanges for the four littoral zone habitats of the Goodwin Islands NERR using the four habitat simulation models. The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT). The exchanges of phytoplankton carbon, total particulate organic carbon (TPOC), dissolved organic carbon (DOC), and total dissolved inorganic nitrogen (TDIN) between a habitat and its two adjacent boundaries were integrated annually and summed to calculate net import (-) or export (+).

	Phytoplankton (gC yr ⁻¹)	TPOC (gC yr ⁻¹)	DOC (gC yr ⁻¹)	TDIN (gN yr ⁻¹)
NVST	-3.9 x 10 ⁷	-4.7 x 10 ⁷	1.4 x 10 ⁸	-1.5 x 10 ⁷
VST	-1.4 x 10 ⁷	-1.7 x 10 ⁸	2.4 x 10 ⁷	-3.1 x 10 ⁶
NVIT	-4.5 x 10 ⁶	-4.7 x 10 ⁷	-1.0 x 10 ⁷	-6.6 x 10 ⁵
VIT	-1.4 x 10 ⁶	-1.4 x 10 ⁷	-1.0 x 10 ⁷	-2.1 x 10 ⁵
TOTALS	-5.9 x 10 ⁷	-2.7 x 10 ⁸	1.5 x 10 ⁸	-1.9 x 10 ⁷

(NVST) predicted imports of phytoplankton C and TPOC equal to $-3.9 \times 10^7 \text{ gC yr}^{-1}$ and $-4.7 \times 10^7 \text{ gC yr}^{-1}$, respectively, from the surrounding boundary environments. The NVST habitat exported DOC to the estuary ($1.4 \times 10^8 \text{ gC}$) and imported TDIN ($-1.5 \times 10^7 \text{ gN}$; Table 5). The vegetated subtidal habitat model (VST) also predicted annual imports of phytoplankton and TPOC equal to $-1.4 \times 10^7 \text{ gC}$ and $-1.7 \times 10^8 \text{ gC}$, respectively. The VST annually exported $2.4 \times 10^7 \text{ gC}$ of DOC to the surrounding habitats and imported $-3.1 \times 10^6 \text{ g TDIN}$ (Table 5). The nonvegetated intertidal habitat model (NVIT) predicted annual imports of $-4.5 \times 10^6 \text{ g}$ phytoplankton C, $-4.7 \times 10^7 \text{ g}$ TPOC, $-1.0 \times 10^7 \text{ g}$ DOC, and $-6.6 \times 10^5 \text{ g TDIN}$ (Table 5). The vegetated intertidal habitat model (VIT) predicted that the marsh annually imports $-1.4 \times 10^6 \text{ g}$ phytoplankton C, $-1.4 \times 10^7 \text{ g}$ TPOC, $-1.0 \times 10^7 \text{ g}$ DOC, and $-2.1 \times 10^5 \text{ g TDIN}$. In order to assess the interactions between the Goodwin Islands littoral zone and the surrounding estuary the annual total exchanges were summed among the habitats. The totals that were calculated using the four habitat models provide annual imports of phytoplankton C ($-5.9 \times 10^7 \text{ gC}$), TPOC ($-2.7 \times 10^8 \text{ gC}$), and TDIN ($-1.9 \times 10^7 \text{ gN}$) and an annual export of DOC ($1.5 \times 10^8 \text{ gC}$) for the littoral zone of the Goodwin Islands NERR.

DISCUSSION

Estuarine littoral zone ecosystems occupy a pivotal position between uplands and offshore channels and link these two boundary environments by the exchange of production and particulate and dissolved materials. An understanding of the biogeochemical processes and patterns that exist within the estuarine littoral zone is essential to investigations of the relationships between the littoral zone and the adjacent

watershed. Simulation modeling provides a method to integrate many aspects of ecosystem dynamics and estimate carbon production, nitrogen demand, and vertical and horizontal material exchanges within the estuarine littoral zone over various scales of time and space. This study utilized a series of four habitat models to assess annual ecosystem processes and habitat patterns in the littoral zone of a pristine polyhaline estuarine ecosystem, the Goodwin Islands National Estuarine Research Reserve in the lower Chesapeake Bay, Virginia (Buzzelli Sections 2 and 3).

One of the main objectives of this modeling study was to estimate the annual rate of net primary production by phytoplankton, sediment microalgae, *Zostera marina*, and *Spartina alterniflora* of the Goodwin Islands NERR (Table 2). The net annual rate of phytoplankton production ($66.0 \text{ gC m}^{-2} \text{ yr}^{-1}$) accounted for 15.8% of total annual ecosystem production and was within the range of values reported in the literature (Table 6). The annual chlorophyll *a* biomass curves generated using the subtidal habitat models are similar to long term patterns evident in data collected in the lower York River, Virginia (Batuik, 1992; Buzzelli Section 2). Using regression equations provided in Malone et al. (1986) and Keller (1989) the annual net rate calculated for the mainstem Chesapeake Bay was $20.26 \text{ gC m}^{-2} \text{ yr}^{-1}$ while that calculated for Narragansett Bay, Rhode Island was $101.6 \text{ gC m}^{-2} \text{ yr}^{-1}$, respectively. An empirical model of Narragansett Bay provided an average rate of $91.25 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Keller, 1988) while estimates of the annual rate of net phytoplankton productivity for North Carolina estuaries ranged $52\text{-}500 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Boyer et al., 1993; Mallin, 1994: Table 6).

The net annual sediment microalgal productivity rate predicted by the four habitat models of the Goodwin Islands NERR ranged $101\text{-}169 \text{ gC m}^{-2} \text{ yr}^{-1}$ and accounted for 34.3% of the total annual littoral zone production. The rate in the nonvegetated

Table 6. Summary of annual net production rates (gC m⁻² yr⁻¹) taken from published literature. ¹Estimated using linear regression equation provided, ² Averaged from values provided.

Phototroph/Location	Annual Rate	Literature Source
Phytoplankton		
Chesapeake Bay	20.26 ¹	Malone et al. 1986
Narragansett Bay	101.61	Keller 1989
Narragansett Bay	91.25 ²	Keller 1988
Neuse River, NC	373.4	Boyer et al. 1993
North Carolina Estuaries	52-500	Mallin 1994
Goodwin Islands Models	66.0	This Study
Sediment Microalgae		
Mudflat in England	143.0	Joint 1978
Subtidal in Denmark	89.0	Colijn and DeJong 1984
Marsh in Mississippi	57.4	Sullivan and Moncreiff 1988
Mudflat in Massachusetts	250.0	Gould and Gallagher 1990
Seagrass meadow in Mississippi	339.0	Daenick et al. 1992
Marsh ecosystem in South Carolina	55-234	Pinckney and Zingmark 1993
Goodwin Islands Models	101-169	This Study
<i>Zostera marina</i>		
Shoots in Massachusetts	155-345	Roman and Able 1988
Shoots in Netherlands	160-412	Van Lent and Verschuure 1994
Goodwin Islands Model-Shoots	241.3	This Study
Root-Rhizomes in Netherlands	53-132	Van Lent and Verschuure 1994
Root-Rhizomes in North Carolina	55-102	Kenworthy and Thayer 1984
Goodwin Islands Model-RR	54.2	This Study
<i>Spartina alterniflora</i>		
Shoots in South Carolina	289-875	Dame and Kenny 1986
Shoots in Georgia	749-1421	Dai and Wiegert in press
Goodwin Islands Model-Shoots	830.8	This Study
Root-Rhizomes in South Carolina	945-2178	Dame and Kenny 1986
Root-Rhizomes in Georgia	397-872	Dai and Wiegert in press
Root-Rhizomes in Virginia	270-857	Blum 1993
Root-Rhizomes in New Jersey	880.0	Smith et al. 1979
Goodwin Islands Model-RR	319.7	This Study

intertidal habitat (NVIT) was greater than that of the other three habitats because of the combined effects of light attenuation due to the depth of the overlying water column (NVST and VST habitats) and shading by the canopy biomass (VST and VIT habitats). Light attenuation from depth was reduced in the NVIT habitat because it was inundated only 46% of the time over the third year of simulation (11,614 of 46,720 time steps). The effects of canopy shading are particularly evident in the differences between the productivity rates in the deeper sand habitat (NVST; 127.6) relative to the shallower seagrass habitat (VST; 101.2). Although sediment microalgal productivity estimates vary with geographic location and habitat, the rates estimated using the Goodwin Islands habitat models were within range of literature sources (Table 6). A shallow nonvegetated subtidal habitat in Denmark averaged $89.0 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Colijn and deJonge, 1984) while mudflats in England and Massachusetts averaged 143.0 and $250.0 \text{ gC m}^{-2} \text{ yr}^{-1}$, respectively (Joint, 1978; Gould and Gallagher, 1990). Sediment microalgal production in a Mississippi seagrass meadow was estimated to be $339.0 \text{ gC m}^{-2} \text{ yr}^{-1}$ while that of a Mississippi *Spartina alterniflora* marsh was $57.4 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Sullivan and Moncreiff, 1988; Daehnick et.al, 1992). Sediment microalgal production over different habitats of the North Inlet, South Carolina salt marsh ecosystem ranged 55-234 $\text{gC m}^{-2} \text{ yr}^{-1}$ (Pinckney and Zingmark, 1993; Table 6).

Zostera marina shoot net annual productivity rate generated by the VST model was $241.3 \text{ gC m}^{-2} \text{ yr}^{-1}$ and was approximately four times that calculated for the epiphytes (55.9) or root-rhizomes (54.2; Table 2). *Zostera marina* community productivity accounted for about 15% of the total production in the littoral zone of the Goodwin Islands NERR (Fig. 3A). The annual biomass curves for the three carbon state variables related to *Zostera marina* are similar to field data collected in the Goodwin Islands seagrass meadow (Buzzelli Section 3) and are within range of long term data for the lower York River, Virginia (Orth

and Moore, 1986). The Goodwin Islands *Zostera marina* shoot productivity ($\text{gC m}^{-2} \text{yr}^{-1}$) was within range of values reported from Massachusetts (155-345) (Roman and Able, 1988) and the Netherlands (160-412) (van Lent and Verschuure, 1994) (Table 7). The Goodwin Islands *Zostera marina* root-rhizome productivity within range of the data reported from North Carolina (55-102; Kenworthy and Thayer, 1984) and the Netherlands (53-132; van Lent and Verschuure, 1994; Table 6).

The processes representing belowground dynamics in the marsh were calibrated and initialized using data collected at the Goodwin Islands NERRS and annual *Spartina alterniflora* shoot and root-rhizome biomass changes predicted using the model were within range of data assembled from the literature (Buzzelli Section 3). *Spartina alterniflora* shoot and root-rhizome productivity were estimated at 830.8 and $319.7 \text{ gC m}^{-2} \text{yr}^{-1}$, respectively, and these rates were similar to the short form shoot and root-rhizome annual productivity rates predicted by Dai and Wiegert (in press) using a canopy model of a Georgia salt marsh (749 and $397 \text{ gC m}^{-2} \text{yr}^{-1}$; Table 6). The similarities between model estimates for the Goodwin Islands *Spartina alterniflora* and those estimated by Dai and Wiegert (in press) result primarily from the inclusion of seasonal cycles of internal carbon translocation in both models (Buzzelli Section 3). *Spartina alterniflora* whole plant production accounted for almost 36% of the total ecosystem production in the Goodwin Islands littoral zone. The shoot productivity estimate agreed with the range of empirical estimates for South Carolina (Dame and Kenny, 1986; Table 6). *Spartina alterniflora* root-rhizome productivity generated using the VIT model of the Goodwin Islands marsh habitat was much lower than those reported for South Carolina (Dame and Kenny, 1986) and New Jersey (Smith et al., 1979) but is within the range of values for Georgia (Dai and Wiegert, in press) and the eastern shore of Virginia (Blum, 1993).

The annual Goodwin Islands phytoplankton nitrogen demand was estimated to be

11.5 gN m⁻² based upon a C:N weight ratio of 5.7 (Table 3). The annual phytoplankton nitrogen uptake rate was estimated to be in excess of nitrogen demand at 15.7 gN m⁻². This disparity may have resulted because phytoplankton state variables have no mechanisms that regulate nitrogen uptake as a function of internal C:N ratio. It is also hypothesized that this difference might reflect a potential for luxury nitrogen uptake by phytoplankton. The differences in the nitrogen requirement of sediment microalgae among the four habitat models resulted from the differences in the net annual carbon productivity rate (Tables 2 and 3).

Nitrogen is taken up from the water column by the shoots and from the sediments by the root-rhizomes of *Zostera marina* (Buzzelli Section 3). Other studies have determined that the sediment is the primary source of nitrogen for eelgrass (Iizumi and Hattori, 1982; Short and McRoy, 1984). Nitrogen is translocated from root-rhizomes to the shoots in order to meet the shoot nitrogen requirement for growth in the Goodwin Islands model and nitrogen uptake by the shoots and root-rhizomes is influenced both by the external concentration and by feedback limitation terms based upon the maximum and minimum C:N ratios of the tissues (Buzzelli Section 3). The difference between the annual nitrogen demand of *Zostera marina* (16.0 gN m⁻² yr⁻¹) and the annual nitrogen uptake (5.95 gN m⁻² yr⁻¹) was attributed to the role of translocation and internal recycling. According to the Goodwin Islands model, about 63% of the macrophyte nitrogen requirement was met through internal recycling. This value is within the range of annual estimates made by Borum et al. (1989; 64%) but is approximately twice the short term rates of translocation measured by Buzzelli and Wetzel (in review; 34%). Later refinements to this model will include bi-directional nitrogen translocation within individual plants as well as carbon and nitrogen translocated from adjacent root-rhizomes connected in the belowground matrix of the eelgrass meadow.

As the case in eelgrass, the whole plant nitrogen requirement for growth of *Spartina alterniflora* ($27.5 \text{ gN m}^{-2} \text{ yr}^{-1}$) was in excess of nitrogen taken up by the macrophyte ($11.5 \text{ gN m}^{-2} \text{ yr}^{-1}$). Approximately 58% of the plant nitrogen requirement was met through internal recycling and these results agree with the 54% estimated in an empirical study in a Georgia marsh (Hopkinson and Schubauer, 1984). Further field and laboratory studies should include the determination of the actual short and long term rates of carbon and nitrogen uptake and translocation in *Spartina alterniflora* using photophysiological methods, carbon and nitrogen stock assessments, and the stable isotope ^{15}N as a tracer. A refinement that is being made to the model is the inclusion of bi-directional translocation of nitrogen to synchronize with seasonal carbon translocation (Buzzelli Section 3).

Despite the fact that the VIT is the smallest habitat, the combined annual production of phytoplankton, sediment microalgae, and *Spartina alterniflora* ($1116 \times 10^6 \text{ gC}$) accounted for 43.1% of total in the littoral zone of the Goodwin Islands NERR (Table 4). Over 80% of the intertidal primary production and 34.1% of the total for the littoral zone was attributable to *Spartina alterniflora* (Fig. 3A). Because the C:N ratio of *Spartina alterniflora* shoots and root-rhizomes is 7-10 times greater than that of the phytoplankton or sediment microalgae, the vegetated intertidal habitat annual nitrogen demand is a small fraction of the total ecosystem nitrogen demand (Table 4). Conversely, the primary production of the phytoplankton and sediment microalgae of the nonvegetated subtidal habitat (NVST) was only 28.6% of the total production in the littoral zone of the Goodwin Islands NERR although it is the largest of the four habitats (Table 4). The NVST required 51.7% of the total littoral zone nitrogen demand due to the low C:N ratio of its constituent producers. The annual C production by the vegetated subtidal habitat (VST; $562 \times 10^6 \text{ gC}$) was approximately half that of the vegetated intertidal habitat ($1116 \times 10^6 \text{ gC}$) but the

annual nitrogen demand and fraction of total ecosystem nitrogen requirement were similar (44×10^6 vs 47×10^6 gN). Of the four littoral zone habitats the nonvegetated intertidal habitat had the least influence upon the annual ecosystem carbon production (6.6%) and nitrogen requirement (11.9%).

All the habitat carbon and nitrogen process estimates listed above are dependent upon the size and composition of the habitats and could potentially differ if these characteristics should change. For discussion purposes, two case scenarios were developed and Table 7 is provided for comparison to Table 4. In the first case, the habitat C and N budgets were calculated as above except that the productivity and nitrogen demand of the *Zostera marina* community were removed to simulate historical times of seagrass absence (Table 7). When eelgrass is removed the ecosystem loses 420×10^6 gC yr⁻¹, the subtidal habitats account for approximately 10% less of the total ecosystem production, and the marsh habitat increases its fraction to 51.5% (Table 7). The NVST, NVIT, and VIT habitats all increase in their fraction of total ecosystem nitrogen demand when eelgrass is removed (Table 7). In the second case the entire subtidal environment was assumed to be vegetated. When the seagrass meadow was extended it caused a 33% increase in total ecosystem primary production (2558 vs 3816 gC yr⁻¹). The subtidal habitat increased to 66% and the intertidal marsh decreased to 29% of the total ecosystem net primary production (Table 7). The subtidal fraction of total annual nitrogen demand increased slightly over the current estimates (Table 7). These results suggest that the seagrass meadow is a significant source of primary production in the Goodwin Islands NERR. In order to thoroughly investigate the impact potential changes in habitat size and composition

Table 7. Estimates of net annual carbon production and nitrogen demand of each of the four littoral zone habitats of the Goodwin Islands NERR using the four habitat simulation models. The top section estimates carbon and nitrogen components when the productivity due to *Zostera marina* was removed. NVST is shown as outside or inside positions. The bottom section assumes that the entire subtidal environment is vegetated by *Zostera marina*. Compare these results to Table 4.

Habitat	Size (ha)	Percent of Total Size	Annual C Production gC	Percent of Total C Production	Annual N Demand gN	Percent of Total N Demand
NVST _{out}	420	51.9%	740 x 10 ⁶	34.2%	130 x 10 ⁶	61.7%
NVST _{in}	120	18.5%	140 x 10 ⁶	6.5%	3.2 x 10 ⁶	1.5%
NVIT	100	12.3%	170 x 10 ⁶	7.9%	30 x 10 ⁶	14.2%
VIT	85	11.1%	1116 x 10 ⁶	51.5%	47 x 10 ⁶	22.6%
NVST	na	na	na	na	na	na
VST	540	70.4%	2530 x 10 ⁶	66.3%	197 x 10 ⁶	71.8%
NVIT	100	12.3%	170 x 10 ⁶	4.5%	30 x 10 ⁶	10.1%
VIT	85	11.1%	1116 x 10 ⁶	29.3%	47 x 10 ⁶	17.4%

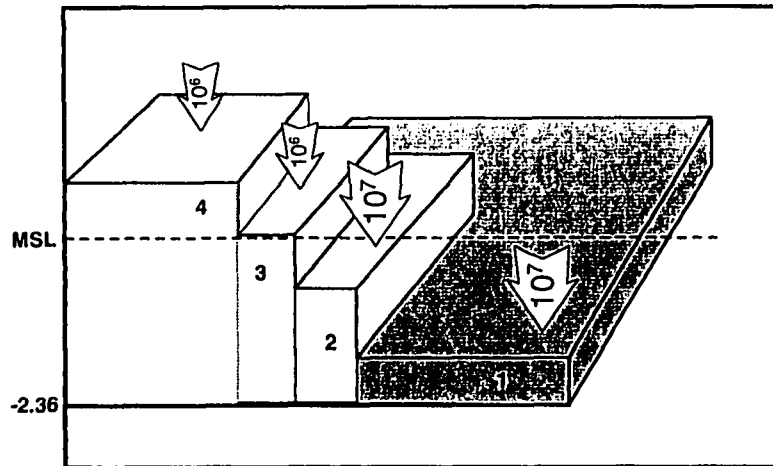
have upon ecosystem dynamics the habitat models themselves must be re-calibrated, initialized, and the simulations performed. It is important to remember that *Zostera marina* shoots are a sink for water column DIN and if the seagrass is removed or extended it could have profound effects upon the DIN dynamics of the Goodwin Islands NERR.

Figure 4 A-D depicts the annual net exchanges for each habitat and water column constituent. An arrow into the habitat denotes a net annual import into the habitat from the adjacent boundaries while an arrow out of a habitat represents a net export of the constituent across its two boundaries. The subtidal net DOC production and export were caused by the comparatively large phytoplankton biomass in the subtidal habitats (Fig. 4A and 4C). The intertidal net DOC imports resulted from the decreased exudation and import of phytoplankton as compared to the subtidal habitat models (Fig. 4A and 4C). Over an annual cycle the nonvegetated intertidal habitat was inundated 46% of the time while the vegetated intertidal habitat was inundated only 25% of the time. The decreased inundation time and phytoplankton import of the intertidal habitats relative to the subtidal habitats did not translate to decreased TPOC import into the intertidal habitats (Table 5 and Fig 4B). The vegetated subtidal habitat imported the greatest TPOC mass annually (-1.7×10^8 gC) while the other three habitats imported similar amounts of TPOC (Table 5 and Fig. 4B). All four habitats imported dissolved inorganic nitrogen and the annual TDIN imported was correlated to the annual phytoplankton mass imported (Fig. 4A and 4D).

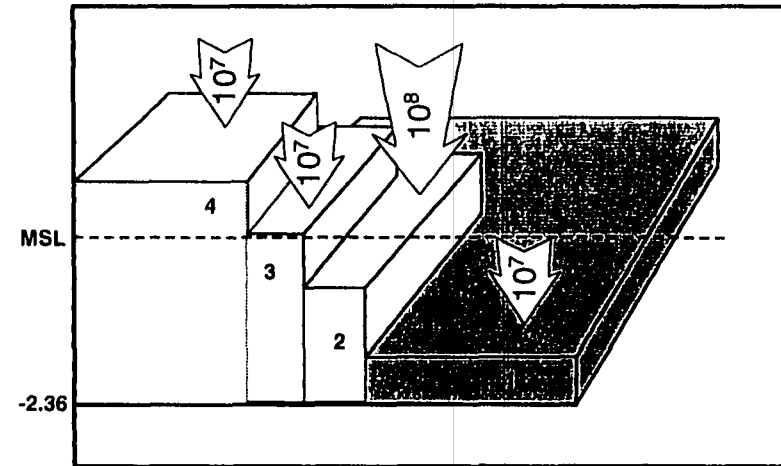
Source/sink scenarios were investigated using the annual fluxes across the individual boundaries of each habitat rather than using the annual net import or export. It appears from the model results that the outermost nonvegetated subtidal habitat (NVST) is a material source and conduit for the Goodwin Islands NERR ecosystem. The NVST produces surplus phytoplankton biomass that can be transported to the other habitats. In situ subtidal phytoplankton productivity is the basis for much of the material flux predicted

Figure 4. Comparison of the annual net exchanges of (A) total phytoplankton, (B) total particulate organic carbon, (C) dissolved organic carbon, and (D) total dissolved inorganic nitrogen. (A-C) are in units of gC yr^{-1} while (D) is in gN yr^{-1} . An arrow pointing into a habitat denotes a net annual import of the water column constituent while an arrow pointing out denotes a net annual export.

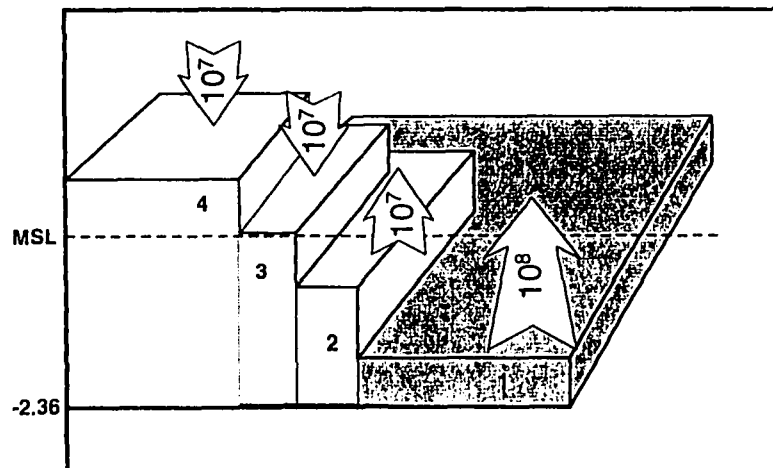
(A) Annual Net Total Phytoplankton Exchange (gC yr^{-1})



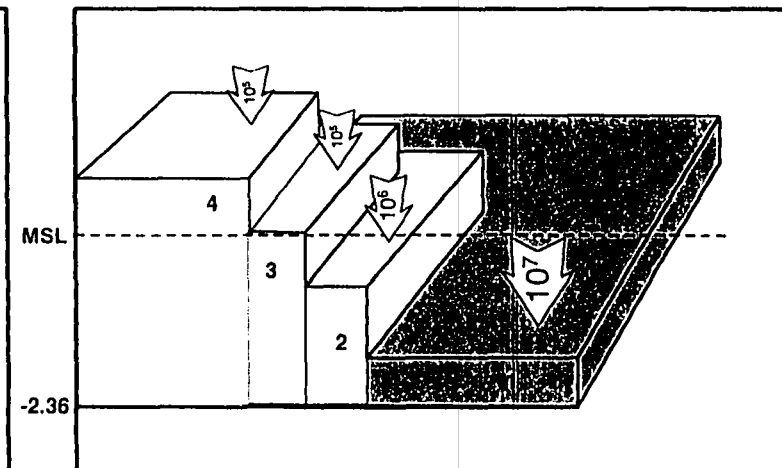
(B) Annual Net Total POC Exchange (gC yr^{-1})



(C) Annual Net DOC Exchange (gC yr^{-1})



(D) Annual Net Total DIN Exchange (gN yr^{-1})



by the habitat simulation models. Phytoplankton productivity leads to increased DOC directly through exudation and indirectly through POC production and subsequent hydrolysis (Buzzelli Section 3). DOC is the material that is remineralized to TDIN in the models and TDIN concentrations influence phytoplankton productivity to complete the cycle. The NVST habitat annually exports 10% more TDIN across its boundary with the VST than the combined import of the other three habitats. Most of the DIN exported by the NVST is derived from in situ phytoplankton production because there were minimal effects of altered channel boundary DIN concentration on NVST phytoplankton dynamics (Buzzelli, unpublished data). Based upon these results the NVST is a phytoplankton, TDIN, and DOC source to the other habitats. The VST is a source of phytoplankton and DOC but a sink for TPOC (Fig. 4B). The intertidal habitats are sinks for TPOC, DOC, and TDIN derived from the subtidal habitats.

The annual TDIN import (gN yr^{-1}) into the four habitats were summed and divided by the total ecosystem annual nitrogen demand (gN yr^{-1}) to calculate the fractional supply. It was estimated that 7.7% of the total ecosystem nitrogen demand is met through water column import. The remaining 92.3% of the ecosystem nitrogen requirement must come from recycling within the sediment environment and macrophytes. Intensive field studies conducted at the Goodwin Islands NERR suggest that the subtidal sediment environment plays a significant role in ecosystem nitrogen cycling (Moore, 1996). The vegetated subtidal habitat traps suspended organics which are deposited into the sediment and remineralized. These models require complete suites of sediment biogeochemical state variables and process equations to better represent the interactions between primary production, material deposition, and biogeochemical cycling in shallow coastal ecosystems (Buzzelli Section 3). Although these models include heterotrophic processes (i.e. respiration), they are autotrophic in nature because of the net annual productivity of the

phototrophs and the annual TDIN imports of each of the habitats. But many heterotrophs are abundant in the water column and sediment environments of the Goodwin Islands NERR including bacteria, zooplankton, meiofauna, worms, molluscs, and resident and migratory crustaceans and fishes. The heterotrophic groups should be included prior to assessing the trophic nature of the Goodwin Islands NERR and the Chesapeake Bay littoral zone. The secondary productivity within the different littoral zone habitats represent a vehicle to transfer energy and nutrients between the phototrophs and higher trophic levels and provide additional mechanisms to link the habitats in time and space.

The habitat models are currently being used to investigate potential change in the littoral zone of the Goodwin Islands NERR. The models are being used to assess the potential interactions between water quality (chlorophyll *a*, suspended solids, inorganic nitrogen) and the dynamics of the eelgrass community. The models are also being used to explore the possible effects that significant increases or decreases in the distribution and abundance of the seagrass or marsh habitats might have upon estimates of ecosystem primary production and material exchange. These models were designed to have their output coupled to coarser scale models of water quality in the Chesapeake Bay watershed (Cерco and Cole, 1993). This study provides a simulation and geographic foundation upon which to base further shorter (days-months) or longer term (10's to 100's years) analyses of ecosystem processes and habitat patterns in the littoral zone of Chesapeake Bay.

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Section 5

SUMMARY AND SYNTHESIS

The primary objective of this doctoral research project was to use mechanistic modeling and landscape ecology to analyze habitat and ecosystem primary production and material flux in the littoral zone of the Goodwin Islands National Estuarine Research Reserve (NERR) in the lower Chesapeake Bay. Because landscape ecology is concerned with the structure, function, and change associated with heterogeneous systems, ecological modeling was employed as a technique to integrate research methods in the analysis of ecosystem spatial dynamics. The goals of this doctoral research project were to, (1) develop an integrative research framework with which to analyze coastal zone ecosystem dynamics, and, (2) describe and investigate the emergent ecosystem properties of the Goodwin Islands NERR. The three research sections of this dissertation addressed these research goals (Sections 2–4).

Section 2 of this dissertation reviewed the habitat distribution and general ecological characteristics of the Goodwin Islands NERR. Although there is considerable information in Section 2 including the distribution and abundance of primary producers and sediment nutrient conditions, the data base is far from complete. Specifically, the biogeochemical rate processes that are responsible for the habitat patterns that emerge must be thoroughly investigated. These processes include photosynthesis, respiration, nitrogen uptake, and nitrogen remineralization in both the water column and the sediment environments. There are ongoing studies that measure rates of carbon and nitrogen cycling in cores incubated under both light and dark conditions trying to link fine scale experimentation with coarser scale intensive sampling and monitoring (I.C. Anderson and K.A. Moore, SMS-VIMS). Section 2 was essential as a starting point because it provided valuable information on ecosystem structure and composition used to develop a series of simulation models of habitat primary productivity and nitrogen cycling.

Much of the field and literature data assembled were used as calibration or validation information in model development and verification (Section 3). Section 3

presented a unique framework with which to investigate coastal ecosystem dynamics. Most spatial models of ecosystem processes assume a rectangular grid of ecosystem components. The series of habitat models developed in this study are concentrically arranged in space and flood and ebb tidal water traverses the habitats in a specific sequence. Adjacent habitats are linked both hydrodynamically and ecologically through the exchange of water volume, phytoplankton, and dissolved and particulate suspended materials. The models were designed to integrate scales of variability, integrate available information, identify where data are missing, investigate the interactions between living resources (i.e. seagrass) and water quality, generate annual habitat and ecosystem carbon and nitrogen budgets, and estimate exchanges across the habitat boundaries in the spatially heterogeneous mosaic (Sections 3 and 4).

These habitat models were used to identify the emergent properties of the Goodwin Islands NERR including the annual nutrient and suspended material budgets. The annual carbon and nitrogen budgets of the habitats depend upon habitat size and composition. The vegetated intertidal habitat is the smallest habitat (85 hectares) but comprises 43% of the annual total. Approximately 35% of the ecosystem annual primary production is by *Spartina alterniflora* and 34% is by sediment microalgae. The annual net productivity rates of microalgae were similar among the four habitats with the subtle differences attributable to differences in light attenuation. The nonvegetated subtidal habitat is the largest (420 hectares), requires 51% of the annual nitrogen demand, and produces 28% of the annual net production for the ecosystem. The large volume and phytoplankton biomass of the nonvegetated subtidal habitat are responsible for these carbon and nitrogen fractions. Eelgrass removal causes a 15% decrease in annual ecosystem primary productivity but when the eelgrass meadow is extended over the entire subtidal bottom the ecosystem productivity increases by 33%. The seagrass habitat also imports the most suspended particulate organic carbon of the four littoral zone habitats and the seagrass meadow is a

significant sink for water column dissolved inorganic nitrogen (Buzzelli, unpublished data). Seagrass meadows have been used as indicators of ecosystem state because they integrate many of the physical, chemical, and biological processes of their environment.

Each habitat exchanges material across each of its two boundaries and it is important to remember that there are four individual habitat models (Section 3). The models were used to assess material exchanges in two different ways (Section 4). The integrated annual flux of a water column constituent between a habitat and its offshore and shoreward boundaries were calculated independently. The independent boundary fluxes were then used to investigate source/sink scenarios among the sequence of four habitats. The difference between the annual fluxes across the offshore and shoreward boundaries of an individual habitat was found to estimate the annual net flux for the habitat. The annual net flux estimate was used to determine the annual import/export properties of each habitat.

The outermost nonvegetated subtidal habitat (NVST) is a material source and conduit for the Goodwin Islands NERR ecosystem. The NVST produces surplus phytoplankton biomass that can be transported to the other habitats. In situ subtidal phytoplankton productivity is the basis for much of the material flux predicted by the habitat simulation models. Phytoplankton productivity leads to increased DOC directly through exudation and indirectly through POC production and subsequent hydrolysis. Dissolved organic carbon is the material remineralized to TDIN in the models and TDIN concentrations influence phytoplankton productivity to complete the cycle. The NVST habitat annually exports 10% more TDIN across its boundary with the VST than the combined import of the other three habitats. Most of the DIN exported by the NVST is derived from in situ phytoplankton production because there were minimal effects of altered channel boundary DIN concentration on NVST phytoplankton dynamics (Buzzelli, unpublished data). Based upon these results the NVST is a phytoplankton, TDIN, and DOC source to the other habitats. The VST is a source of phytoplankton and DOC but a

sink for TPOC. The intertidal habitats are sinks for TPOC, DOC, and TDIN derived from the subtidal habitats.

All four habitats imported all of the water column constituents annually except a net annual export of DOC from the subtidal habitats. The subtidal net DOC production and export were caused by their comparatively large phytoplankton biomass. The intertidal net DOC imports resulted from the decreased exudation and import of phytoplankton as compared to the subtidal habitat models. Over an annual cycle the nonvegetated intertidal habitat was inundated 46% of the time while the vegetated intertidal habitat was inundated only 25% of the time. The decreased inundation time and phytoplankton import of the intertidal habitats relative to the subtidal habitats did not translate to decreased TPOC import into the intertidal habitats. The vegetated subtidal habitat imported the greatest TPOC mass annually (-1.7×10^8 gC) while the other three habitats imported similar amounts of TPOC. All four habitats imported dissolved inorganic nitrogen and the annual TDIN imported was related to the annual phytoplankton mass imported.

Sections 2–4 addressed the composition, structure, and function of the littoral zone of the Goodwin Islands NERR. Change in system structure and function is the final priority of landscape ecology and these models are currently being used to investigate potential change in the ecosystem properties of the Goodwin Islands NERR. Listed below are several questions related to changes in the estuarine littoral zone ecology.

- What are the relationships between increased DIN loading and eelgrass community carbon productivity and nitrogen demand?
- What are the relationships between increased DIN loading, epiphytic growth, and shading effects in the eelgrass meadow?
- How does a constant DIN loading differ when pulsed at regular or irregular intervals into the littoral zone?

- What influence would changes in habitat size and composition have upon the habitat and ecosystem material exchange properties? What if the seagrass component of the vegetated subtidal habitat is lost or increased in coverage? What effects would a loss of vegetated marsh have upon habitat and ecosystem flux characteristics?

The models are useful tools to address these and other management oriented environmental scenarios. Although the models and the ecosystem characteristics derived from them provide insights into the functioning of the estuarine littoral zone, it would be difficult to extend these insights across the entire Chesapeake Bay because there are some important ecological components that have not been included (Section 3). The hydrodynamic models are driven exclusively by tidal processes with no influence of advective or stochastic factors. Currently there are four individual habitat models and ideally these four models would be linked in model space and time to completely couple their associated inputs and outputs. A deficiency of these models is the lack of sediment related state variables although they do include sediment microalgae and macrophytes. State variables and processes related to sediment elevation, material resuspension and deposition, in situ decay, and nutrient regeneration must be included to more accurately represent ecological dynamics in shallow coastal systems. The current models support this notion because the models predict that over 90% of the ecosystem nitrogen demand comes from recycled nitrogen (Section 4). The sediment provides a source of inorganic nitrogen for both macrophytes and the water column because of its increased nutrient concentrations and rates of recycling (rem mineralization, nitrification/denitrification). Another drawback to the models is the lack of state variables and process equations for heterotrophic groups including bacteria, microscopic and macroscopic invertebrates, and fishes. An analysis of ecosystem trophic structure and dynamics is not warranted without consideration for these ecosystem components. The heterotrophs could represent a significant source of inorganic

nitrogen and a sink for particulate organic carbon within the various habitats and could serve as additional mechanism to link the littoral zone habitats in time and space.

This doctoral research project has provided an integrative framework for the analysis of coastal zone ecological dynamics. This project has also created a foundation for ongoing and future research on the Goodwin Islands NERR. The determination of field data and habitat structure, the literature source lists that have been assembled, and the digitized habitat coverages of the preliminary GIS help to establish this research foundation. This project provides a mechanism to investigate the dynamics within the estuarine littoral zone. An understanding of dynamics within the littoral zone provides a better understanding of the function of the littoral zone in the Chesapeake Bay landscape.

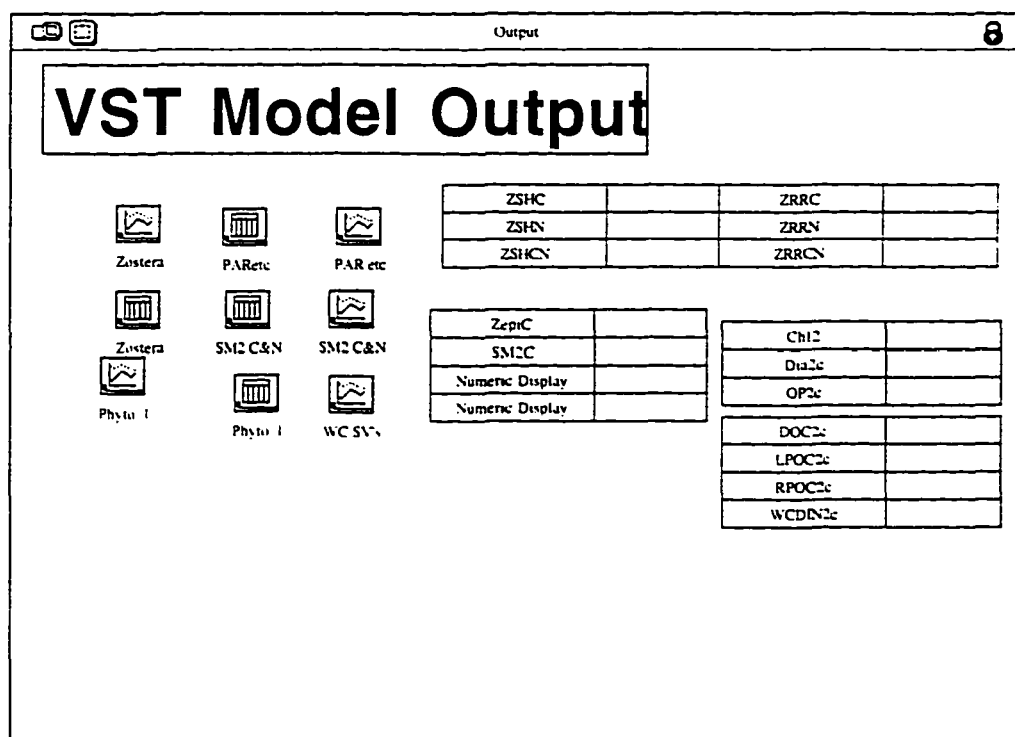
Section 6

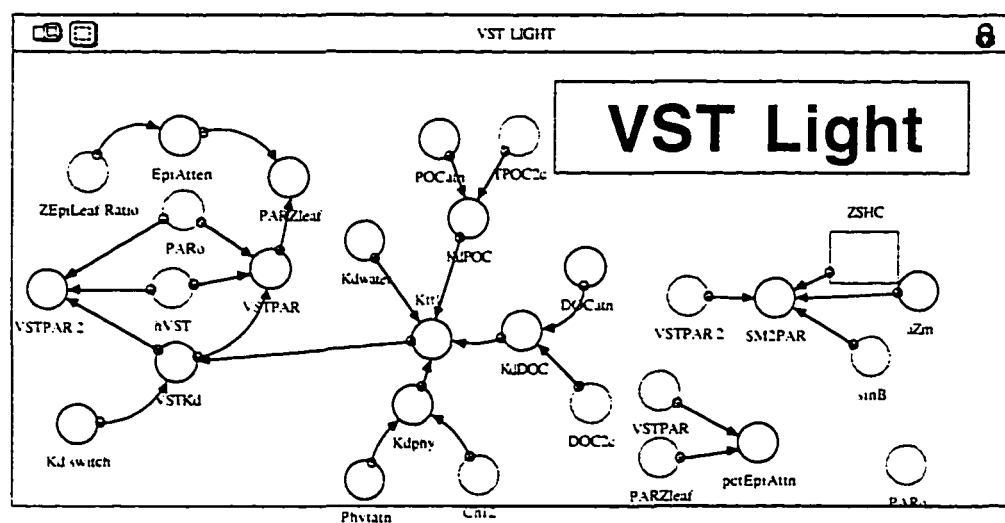
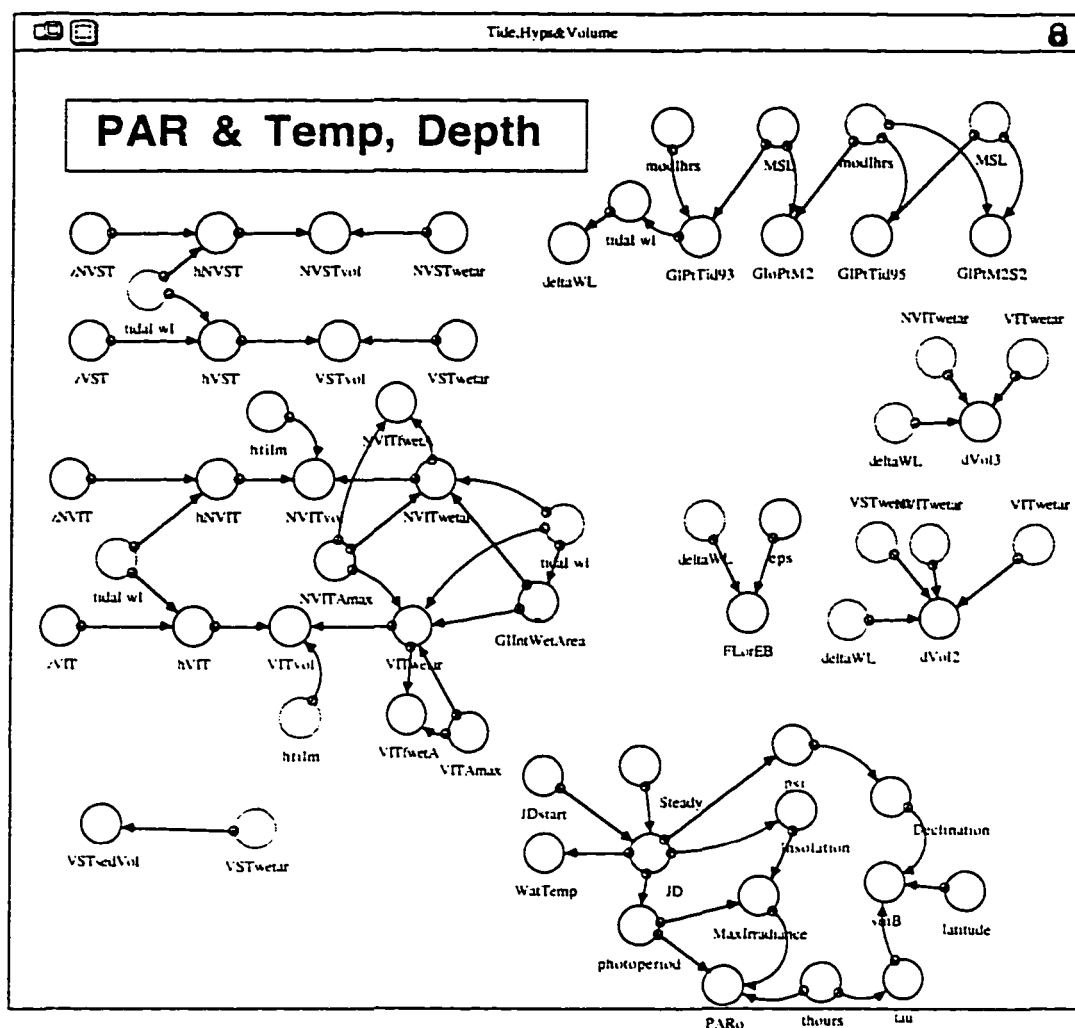
APPENDICES

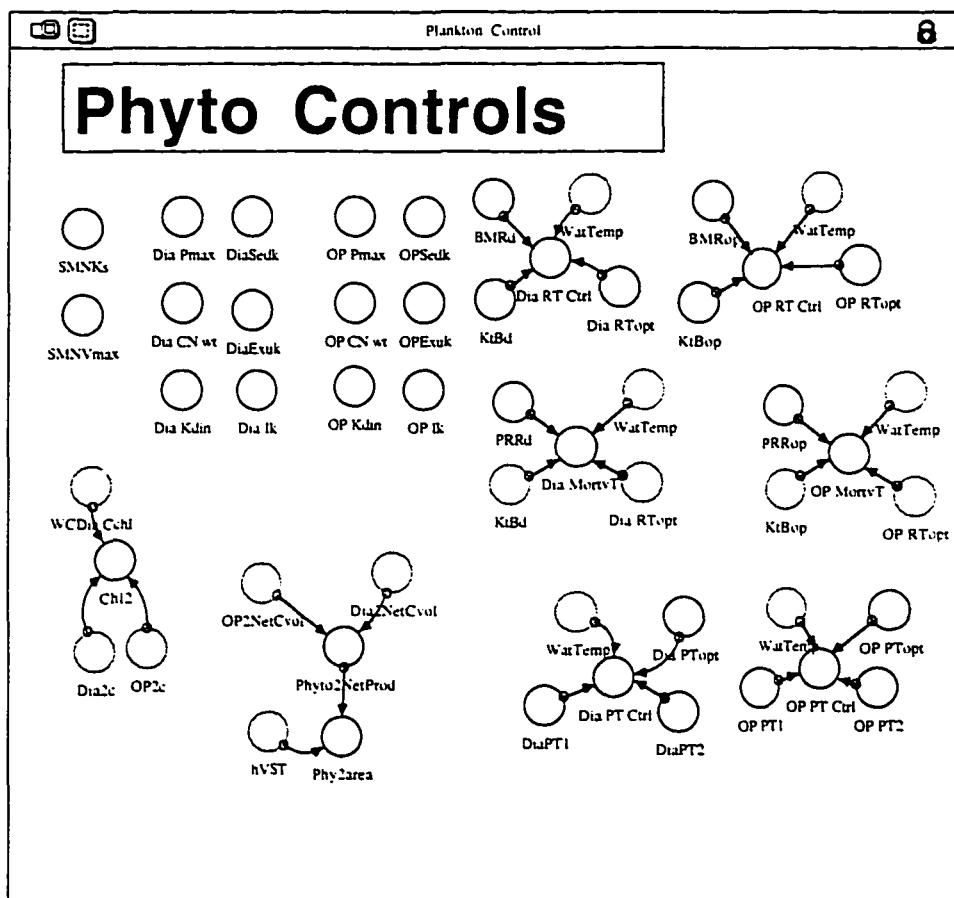
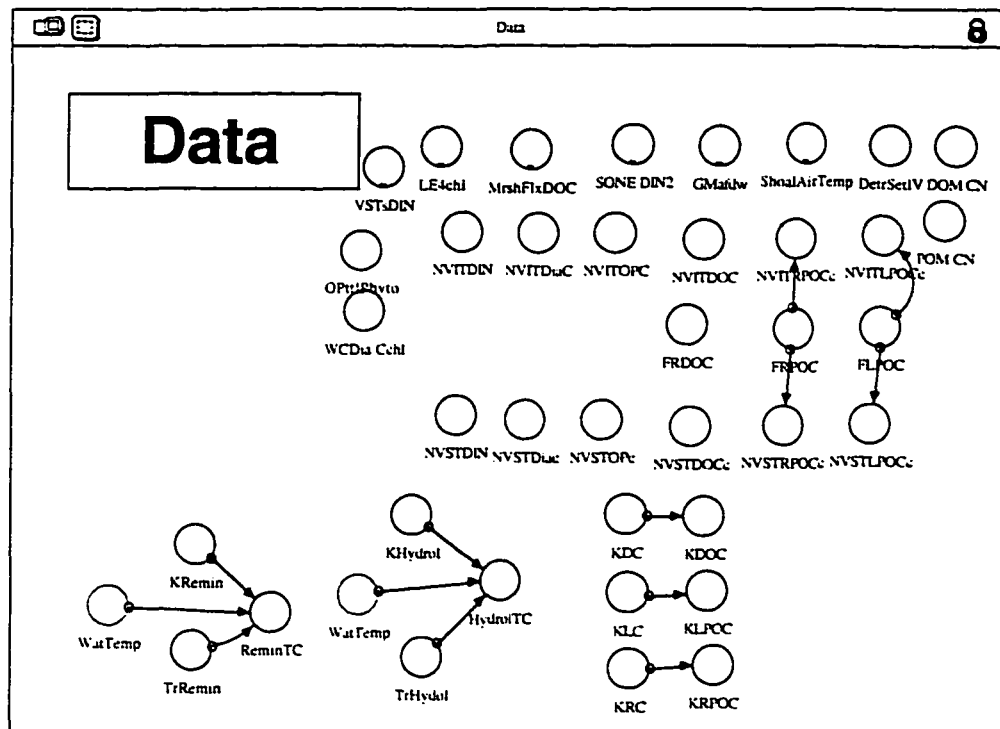
Goodwin Islands Vegetated Subtidal Habitat Submodel.

Created by Chris Buzzelli and Mark Meyers. Transferred from the Goodwin Islands Linked Littoral Zone Spatial Ecosystem Model.
September 1995

TimeSpecs: DAYS

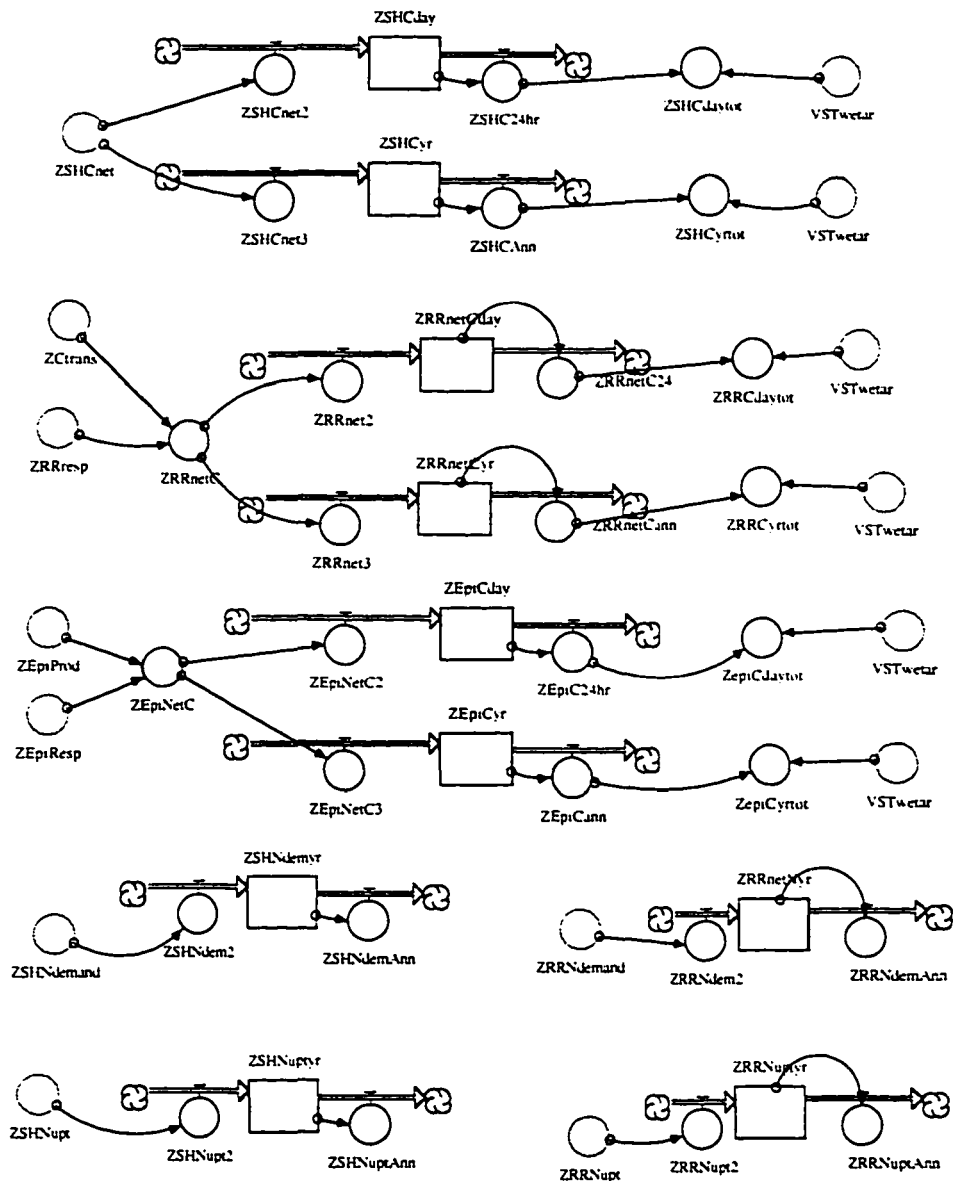






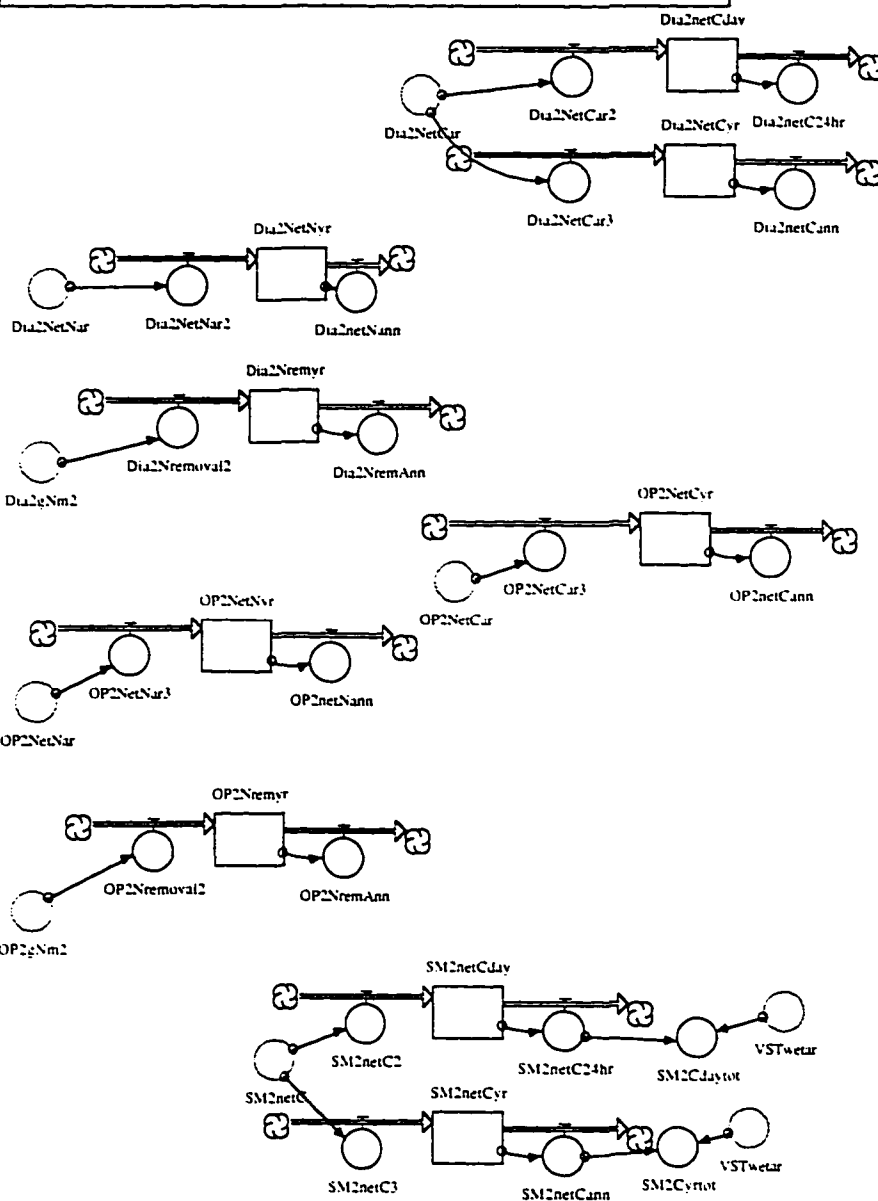


Zostera C&N Integrators

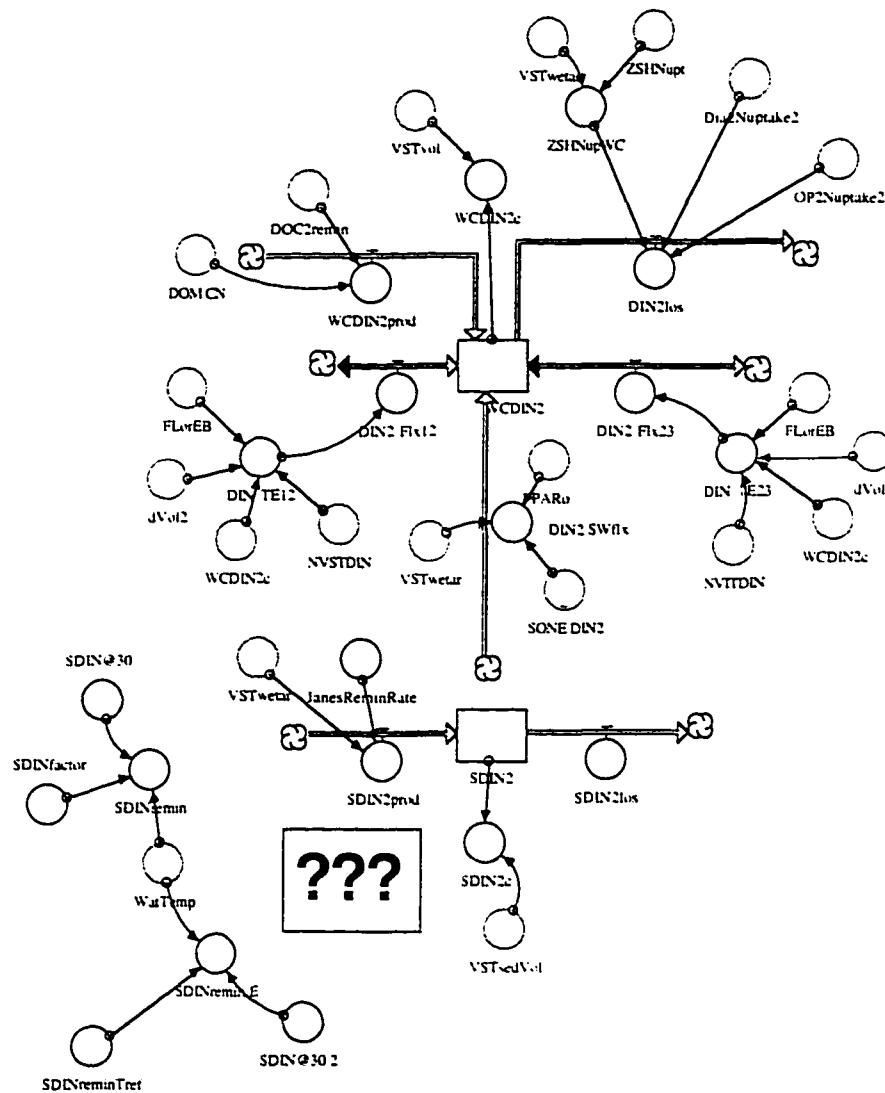




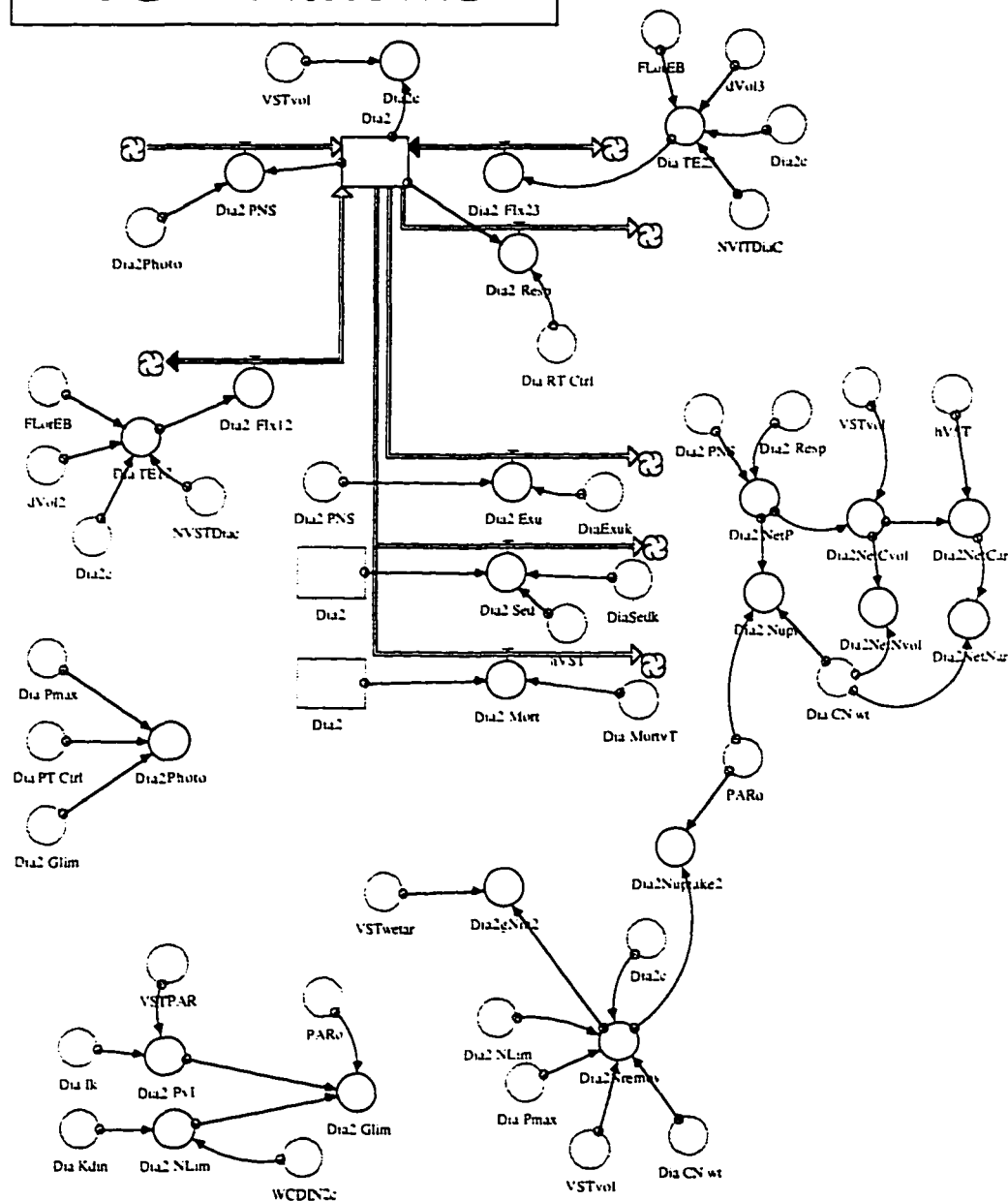
Phyto and SM C&N Integrators

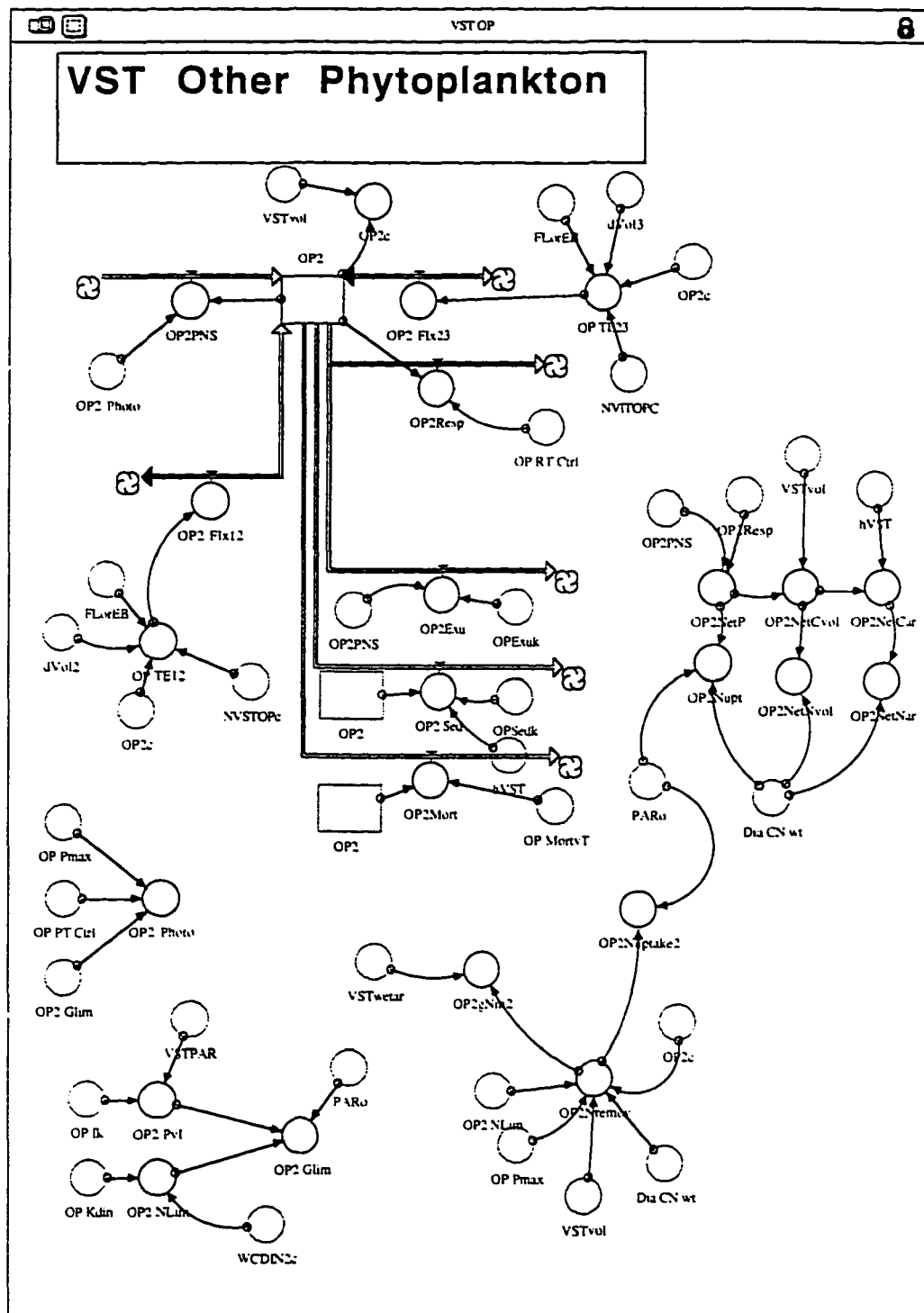


OP₂Nupt Dia₂Nupt

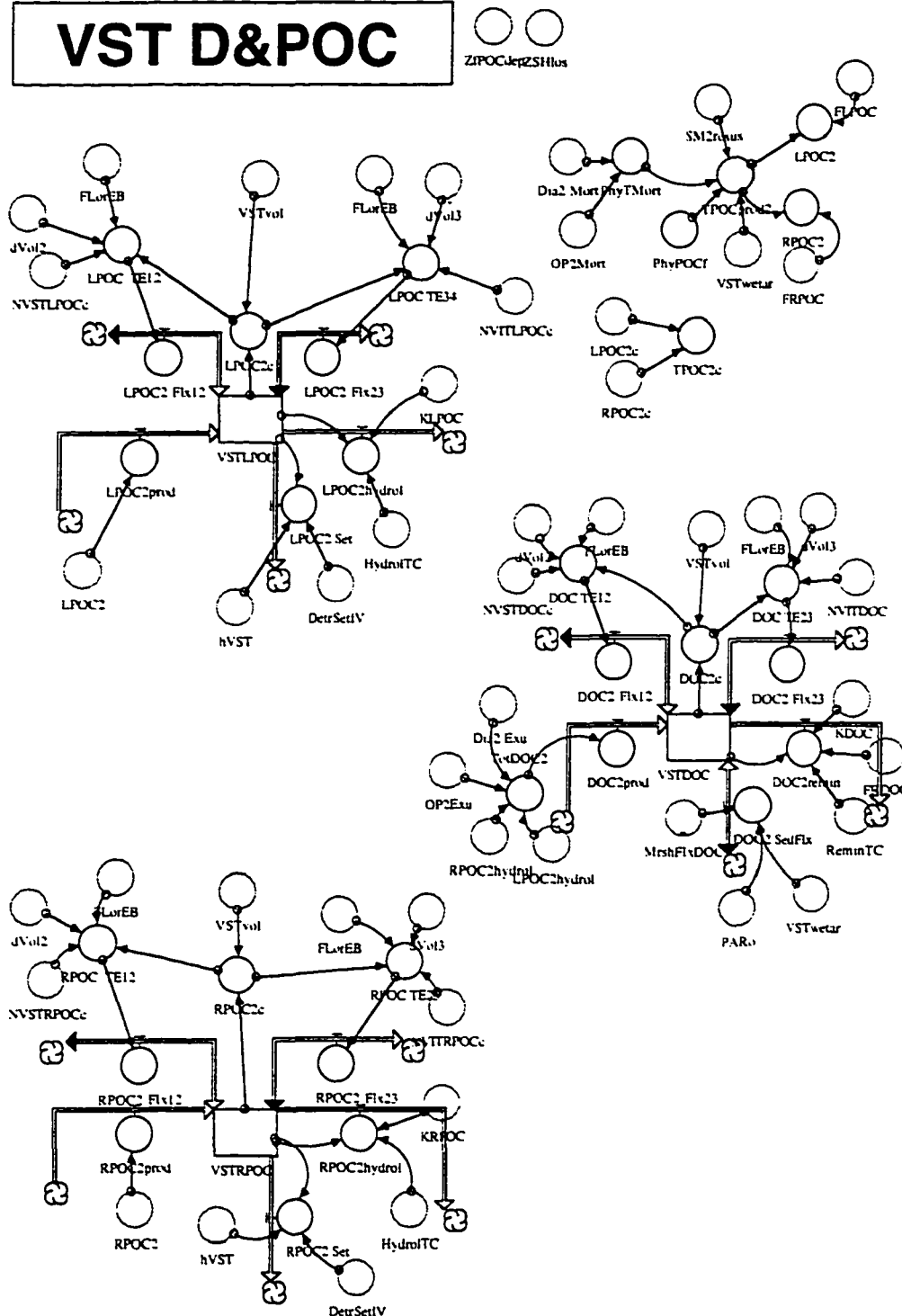


VST Diatoms



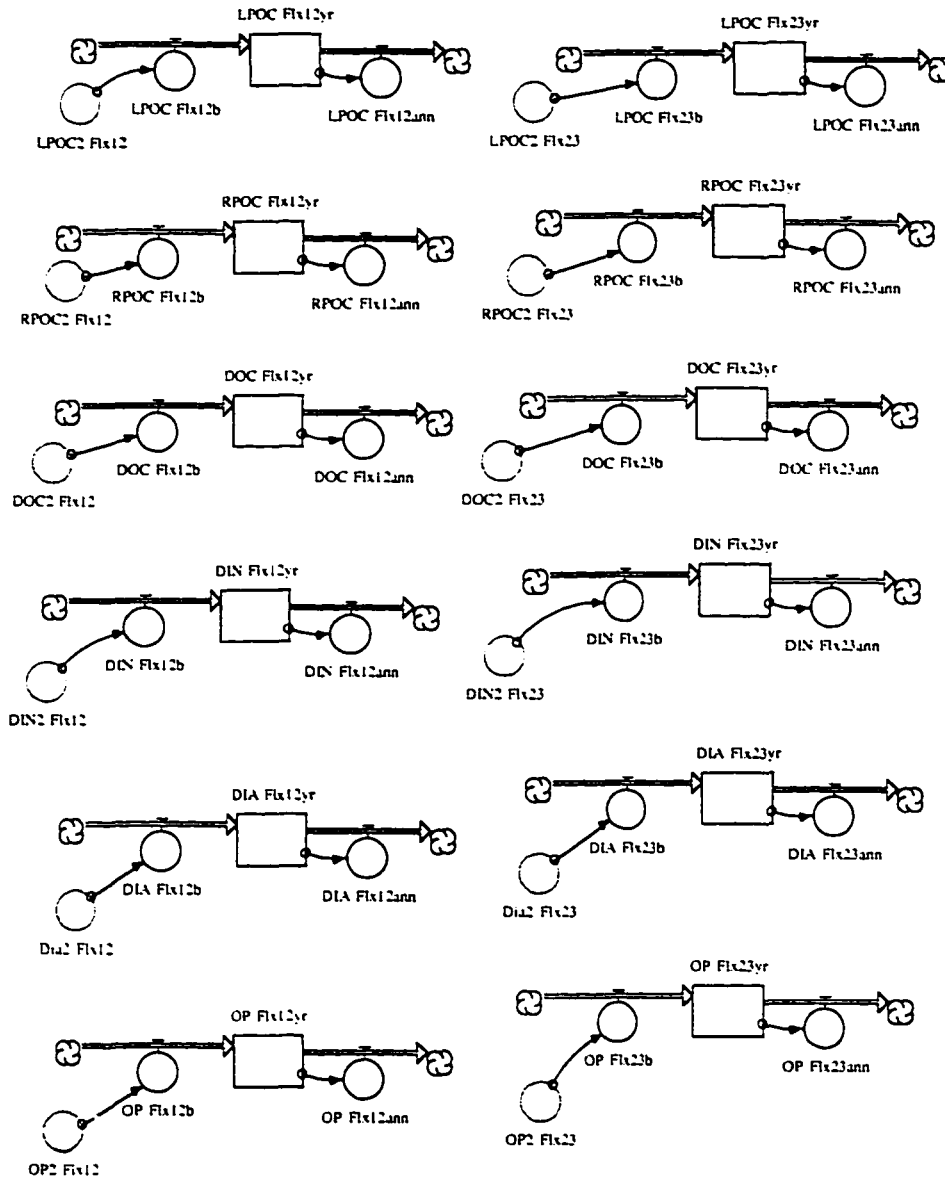


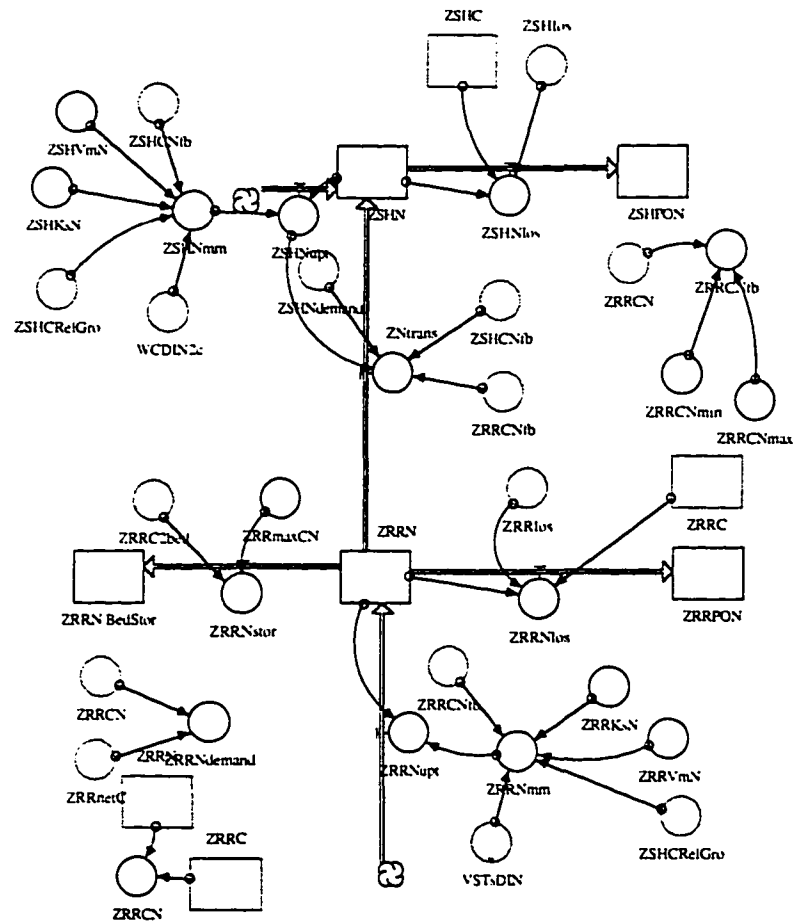
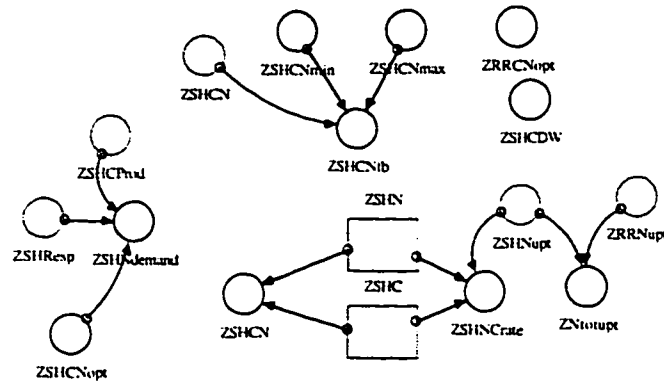
VST D&POC





Exchange Integrators





[illegible]

Vegetated Subtidal Habitat Model Equations

PHYTO AND SM C&N INTEGRATORS

$$\text{Dia2netCday}(t) = \text{Dia2netCday}(t - dt) + (\text{Dia2NetCar2} - \text{Dia2netC24hr}) * dt$$

$$\text{INIT Dia2netCday} = 0.0$$

DOCUMENT: Daily Diatom Productivity. (gC/m²/d) This accumulates (or loses?) net diatoms each DT and spits out daily values.

$$\text{Dia2NetCar2} = \text{Dia2NetCar}$$

DOCUMENT: Diatom Net C Production, VST. (gC/m²/d).

$$\text{Dia2netC24hr} = \text{PULSE}(\text{Dia2netCday}, 2, 1)$$

DOCUMENT: Integrated Daily Diatom Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$$\text{Dia2NetCyr}(t) = \text{Dia2NetCyr}(t - dt) + (\text{Dia2NetCar3} - \text{Dia2netCann}) * dt$$

$$\text{INIT Dia2NetCyr} = 0.0$$

DOCUMENT: Annual Diatom Productivity. (gC/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$$\text{Dia2NetCar3} = \text{Dia2NetCar}$$

DOCUMENT: Diatom Net C Production, VST. (gC/m²/d).

$$\text{Dia2netCann} = \text{PULSE}(\text{Dia2NetCyr}, 365, 365)$$

DOCUMENT: Integrated Annual Diatom Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$$\text{Dia2NetNyr}(t) = \text{Dia2NetNyr}(t - dt) + (\text{Dia2NetNar2} - \text{Dia2netNann}) * dt$$

$$\text{INIT Dia2NetNyr} = 0.0$$

DOCUMENT: Annual Diatom Productivity. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$$\text{Dia2NetNar2} = \text{Dia2NetNar}$$

DOCUMENT: Diatom Net N Production, VST. (gN/m²/d).

$$\text{Dia2netNann} = \text{PULSE}(\text{Dia2NetNyr}, 365, 365)$$

DOCUMENT: Integrated Annual Diatom Net Production. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$$\text{Dia2Nremyr}(t) = \text{Dia2Nremyr}(t - dt) + (\text{Dia2Nremoval2} - \text{Dia2NremAnn}) * dt$$

$$\text{INIT Dia2Nremyr} = 0.0$$

DOCUMENT: Annual Diatom N Removal. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$$\text{Dia2Nremoval2} = \text{Dia2gNm2}$$

DOCUMENT: Diatom Net N Removal, VST. (gN/m²/d).

$$\text{Dia2NremAnn} = \text{PULSE}(\text{Dia2Nremyr}, 365, 365)$$

DOCUMENT: Integrated Annual Diatom N Removal. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP2NetCyr(t) = OP2NetCyr(t - dt) + (OP2NetCar3 - OP2netCann) * dt$
 INIT $OP2NetCyr = 0.0$
 DOCUMENT: Annual OP Productivity. (gC/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP2NetCar3 = OP2NetCar$
 DOCUMENT: OP Net C Production, VST. (gC/m²/d).

$OP2netCann = PULSE(OP2NetCyr, 365, 365)$
 DOCUMENT: Integrated Annual OP Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP2NetNyr(t) = OP2NetNyr(t - dt) + (OP2NetNar3 - OP2netNann) * dt$
 INIT $OP2NetNyr = 0.0$
 DOCUMENT: Annual OP Productivity. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP2NetNar3 = OP2NetNar$
 DOCUMENT: OP Net N Production, VST. (gN/m²/d).

$OP2netNann = PULSE(OP2NetNyr, 365, 365)$
 DOCUMENT: Integrated Annual OP Net Production. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP2Nremyr(t) = OP2Nremyr(t - dt) + (OP2Nremoval2 - OP2NremAnn) * dt$
 INIT $OP2Nremyr = 0.0$
 DOCUMENT: Annual OP N Removal. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP2Nremoval2 = OP2gNm2$
 DOCUMENT: OP Net N Removal, VST. (gN/m²/d).

$OP2NremAnn = PULSE(OP2Nremyr, 365, 365)$
 DOCUMENT: Integrated Annual OP N Removal. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SM2netCday(t) = SM2netCday(t - dt) + (SM2netC2 - SM2netC24hr) * dt$
 INIT $SM2netCday = 0.0$
 DOCUMENT: Daily Sediment Microalgae Productivity. (gC/m²/d) This accumulates (or loses?) net Sediment Microalgae each DT and spits out daily values.

$SM2netC2 = SM2netC$
 DOCUMENT: Sediment Microalgae Net C Production, VST. (gC/m²/d).

$SM2netC24hr = PULSE(SM2netCday, 2, 1)$
 DOCUMENT: Integrated Daily Sediment Microalgae Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SM2netCyr(t) = SM2netCyr(t - dt) + (SM2netC3 - SM2netCann) * dt$
 INIT $SM2netCyr = 0.0$
 DOCUMENT: Annual Sediment Microalgae Productivity. (gC/m²/yr) This accumulates (or loses?) net

Sediment Microalgae each DT and spits out yearly values.

$SM2netC3 = SM2netC$

DOCUMENT: Sediment Microalgae Net C Production, VST. (gC/m²/d).

$SM2netCann = PULSE(SM2netCyr, 365, 365)$

DOCUMENT: Integrated Annual Sediment Microalgae Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SM2Cdaytot = SM2netC2\text{-}4hr * VSTwet\text{-}ar$

DOCUMENT: Sediment Microalgae 2 C daily total net. (gC/d). The areal rate * the habitat area.

$SM2Cyr\text{-}tot = SM2netCann * VSTwet\text{-}ar$

DOCUMENT: Sediment Microalgae 2 C annual total net. (gC/yr). The areal rate * the habitat area.

DATA

$DetrSetlV = 0.25 \{0.25 * 2 \text{ m/d; WES}=1.0\}$

DOCUMENT: Detritus Settling Velocity. (m/d). From Waterways Experiment Station.

$DOM_CN = 10$

DOCUMENT: Dissolved Organic Matter C:N. (unitless). This is the C:N ratio of water column DOM.

$FLPOC = 0.55$

DOCUMENT: Fraction Labile POC. (unitless). 55% of total POC is labile. From Cerco&Cole.

$FRDOC = 0.0$

DOCUMENT: Fraction Refractory DOC. (unitless). This is the unusable fraction of the DOC. Initially set at 20%.

$FRPOC = 0.45$

DOCUMENT: Fraction Refractory POC. (unitless). 45% of total POC is refractory. From Cerco&Cole.

$Hydro\text{-}lTC = EXP(KHydro\text{-}l * (WatTemp - TrHydro\text{-}l))$

DOCUMENT: Hydrolysis Temperature effect. (unitless). Exponential effect term.

$KDC = 0.010$

DOCUMENT: Constant for Labile Dissolved Carbon Remineralization. (/d). From Cerco & Cole. 1994. {0.01=1/day}

$KDOC = KDC$

DOCUMENT: Constant for Labile Dissolved Carbon Remineralization. (/d). From Cerco & Cole. 1994. Used if different than KDC.

$KHydro\text{-}l = 0.069$

DOCUMENT: Constant for Hydrolysis (unitless?). From Cerco & Cole. Hydrolysis goes from POC to DOC

$KLC = 0.075$

DOCUMENT: Constant for Labile Carbon Hydrolysis to DOC. (/d). Cerco & Cole. 1994: 0.075 (15 d "e-folding" time).

KLPOC = KLC

DOCUMENT: Constant for Labile Carbon Remineralization. (/d). From Cerco & Cole, 1994. Used if different from KLC.

KRC = 0.005

DOCUMENT: Constant for Refractory Particulate Carbon Hydrolysis to DOC. (/d). From Cerco & Cole, 1994.

KRemin = 0.069

DOCUMENT: Constant for Remineralization. (unitless?). From Cerco & Cole. Remineralization takes DOC and makes DON.

KRPOC = KRC

DOCUMENT: Constant for Refractory Particulate Carbon Remineralization. (/d). From Cerco & Cole, 1994. Used if different than KRC.

NVITDiac = 0.165

DOCUMENT: NonVegetated Intertidal Diatom C Conc. (gC/m3). $10 \text{ mg Chla/m}^3 / 1000 * 50 \text{ gC/gChla} * 0.33 \text{ (fraction Diatoms)} = 0.165$

NVITDIN = 5.0

DOCUMENT: NonVegetated Intertidal Water Column DIN Conc. (mmoles/m3). 5 uM taken from Moore GI Intensive.

NVITDOC = 1.0

DOCUMENT: NonVegetated Intertidal DOC. (gC/m3). This is the NVIT (3) boundary DOC concentration for the VST habitat (+). 2.5-11.8 mgC/L referenced in Williams et al. 1992, Bly Creek, SC. Betty's data from EShore, VA = 3.5 gC/m3.

NVITLPOCc = 5*FLPOC

DOCUMENT: NonVegetated Intertidal Labile POC conc. (gC/m3). $5.0 \text{ g/m}^3 * \text{the fraction labile} = 5.0$ from Shoal Run data.

NVITOPC = 0.33

DOCUMENT: NonVegetated Intertidal Diatom C Conc. (gC/m3). $10 \text{ mg Chla/m}^3 / 1000 * 50 \text{ gC/gChla} * 0.67 \text{ (fraction Diatoms)} = 0.33$

NVITRPOCc = 5*FRPOC

DOCUMENT: NonVegetated Intertidal Refractory POC conc. (gC/m3). $5.0 \text{ g/m}^3 * \text{the fraction refractory} = 5.0$ from Shoal Run data.

NVSTDiac = 0.165

DOCUMENT: NonVegetated Subtidal Diatom C Conc. (gC/m3). $10 \text{ mg Chla/m}^3 / 1000 * 50 \text{ gC/gChla} * 0.33 \text{ (fraction Diatoms)} = 0.165$

NVSTDIN = 10

DOCUMENT: NonVegetated Subtidal Water Column DIN Conc. (mmoles/m3). 10 uM taken from Shoal Survey.

NVSTDCC = 0.7

DOCUMENT: NonVegetated Subtidal DOC. (gC/m3). Channel DOC concentration Taken from Ray, Haas & Sieracki, '89; Eldridge & Sieracki, '93. $7E05 \text{ pgC/ml} = 0.7 \text{ gC/m}^3$. This is the NVIT (3) boundary

DOC concentration for the VIT habitat (4). 2.5-11.8 mgC/L referenced in Williams et al. 1992. Bly Creek, SC.

NVSTLPOCc = 5*FLPOC

DOCUMENT: NonVegetated Subtidal Labile POC conc. (gC/m3). 5.0 g/m3* the fraction labile. 5.0 from Shoal Run data.

NVSTOPc = 0.33

DOCUMENT: NonVegetated Subtidal Diatom C Conc. (gC/m3). 10 mg Chla/m3 /1000 * 50 gC/gChla * 0.67 (fraction Diatoms) = 0.33

NVSTRPOCc = 5*FRPOC

DOCUMENT: NonVegetated Subtidal Refractory POC conc. (gC/m3). 5.0 g/m3* the fraction refractory. 5.0 from Shoal Run data.

OPtlPhyto = 0.67

DOCUMENT: Other Plankton:Total Phytoplankton ratio. (unitless). From Ray, Haas & Sieracki, 1989: Table 1. 67% over all size classes.

POM_CN = 10

DOCUMENT: Particulate Organic Matter C:N. (unitless). This is the C:N ratio of water column POM.

ReminTC = EXP(KRemin*(WatTemp-TrRemin))

DOCUMENT: Remineralization Temperature effect. (unitless). Exponential effect term.

TrHydol = 20.0

DOCUMENT: Reference Temperature for Remineralization. (degC).

TrRemin = 20.0

DOCUMENT: Reference Temperature for Remineralization. (degC).

WCDia_Cchl = 50

DOCUMENT: Water Column Diatom C:Chl ratio. (unitless).

GMafdw = GRAPH(TIME)

(0.00, 2.24), (33.2, 2.77), (66.4, 2.46), (99.5, 1.91), (133, 2.01), (166, 3.01), (199, 4.22), (232, 3.18), (265, 3.32), (299, 2.61), (332, 2.21), (365, 1.88)

DOCUMENT: Shoal Survey Guinea Marsh AFDW. (gC/m3). The AFDW of suspended sediment collected biweekly in the lower York River, Guinea Marsh means from 1984-1992 (mgC/L = gC/m3).

LE4chl = GRAPH(TIME)

(0.00, 12.0), (30.4, 19.0), (60.8, 18.0), (91.2, 15.0), (122, 10.0), (152, 8.00), (182, 12.0), (213, 10.0), (243, 7.00), (274, 5.00), (304, 5.00), (335, 3.00), (365, 12.0)

MrshFlxDOC = GRAPH(TIME)

(0.00, 0.00), (33.2, 0.08), (66.4, -0.2), (99.5, -0.35), (133, -0.3), (166, -0.25), (199, -0.3), (232, -0.35), (265, -0.32), (299, -0.3), (332, -0.35), (365, -0.42)

DOCUMENT: Marsh Flux DOC. (gC/m2/d). From Betty Berry's thesis @ EShore, VA landward marshes.

ShoalAirTemp = GRAPH(time)

(0.00, 2.00), (33.2, 5.00), (66.4, 14.0), (99.5, 19.0), (133, 22.0), (166, 25.0), (199, 32.0), (232, 35.0), (265, 25.0), (299, 19.0), (332, 14.0), (365, 10.0)

DOCUMENT: Shoal Air Temperature. (degC). This graph is from actual data collected at Goodwin Islands during 1994. Should include multi-annual means, but now is only 1994.

SONE_DIN2 = GRAPH(TIME)

(0.00, -0.1), (33.2, -0.15), (66.4, -0.173), (99.5, -0.25), (133, -0.3), (166, -0.681), (199, -0.5), (232, -0.483), (265, -0.3), (299, -0.774), (332, -0.5), (365, -0.25)

DOCUMENT: Sone DIN 2, VST. (mmol/m2/d). This is from CBuzz GI SONE flux studies. 1 day = 12 hours.

VSTsDIN = GRAPH(time)

(0.00, 208), (36.5, 80.0), (73.0, 72.0), (110, 124), (146, 226), (182, 375), (219, 166), (256, 235), (292, 232), (328, 294), (365, 213)

DOCUMENT: VST Sediment DIN. (uM). Monthly mean total sediment DIN from Buzzelli thesis at Guinea Marsh.

HABITAT EXCHANGE INTEGRATORS

$DIA_Flx12yr(t) = DIA_Flx12yr(t - dt) + (DIA_Flx12b - DIA_Flx12ann) * dt$

INIT DIA_Flx12yr = 0.0

DOCUMENT: Annual DIA Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$DIA_Flx12b = Dia2_Flx12$

DOCUMENT: Diatom Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of diatoms between the NVST & VST habitats.

$DIA_Flx12ann = PULSE(DIA_Flx12yr, 365, 365)$

DOCUMENT: Integrated Annual DIA Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$DIA_Flx23yr(t) = DIA_Flx23yr(t - dt) + (DIA_Flx23b - DIA_Flx23ann) * dt$

INIT DIA_Flx23yr = 0.0

DOCUMENT: Annual DIA Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$DIA_Flx23b = Dia2_Flx23$

DOCUMENT: Diatom Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of diatoms between the VST & NVIT habitats.

$DIA_Flx23ann = PULSE(DIA_Flx23yr, 365, 365)$

DOCUMENT: Integrated Annual DIA Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$DIN_Flx12yr(t) = DIN_Flx12yr(t - dt) + (DIN_Flx12b - DIN_Flx12ann) * dt$

INIT DIN_Flx12yr = 0.0

DOCUMENT: Annual DIN Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$DIN_Flx12b = DIN2_Flx12$

DOCUMENT: DIN Tidal Exchange between Habitats 1 & 2. (mmoles/d). The physical exchange of DIN between the NVST and VST habitats.

DIN_Flx12ann = PULSE(DIN_Flx12yr,365,365)

DOCUMENT: Integrated Annual DIN Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

DIN_Flx23yr(t) = DIN_Flx23yr(t - dt) + (DIN_Flx23b - DIN_Flx23ann) * dt

INIT DIN_Flx23yr = 0.0

DOCUMENT: Annual DIN Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

DIN_Flx23b = DIN2_Flx23

DOCUMENT: DIN Tidal Exchange between Habitats 2 & 3. (mmoles/d). The physical exchange of DIN between the VST and NVIT habitats.

DIN_Flx23ann = PULSE(DIN_Flx23yr,365,365)

DOCUMENT: Integrated Annual DIN Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

DOC_Flx12yr(t) = DOC_Flx12yr(t - dt) + (DOC_Flx12b - DOC_Flx12ann) * dt

INIT DOC_Flx12yr = 0.0

DOCUMENT: Annual DOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

DOC_Flx12b = DOC2_Flx12

DOCUMENT: DOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of RPOC between the NVST & VST habitats.

DOC_Flx12ann = PULSE(DOC_Flx12yr,365,365)

DOCUMENT: Integrated Annual DOC Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

DOC_Flx23yr(t) = DOC_Flx23yr(t - dt) + (DOC_Flx23b - DOC_Flx23ann) * dt

INIT DOC_Flx23yr = 0.0

DOCUMENT: Annual DOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

DOC_Flx23b = DOC2_Flx23

DOCUMENT: DOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of DOC between the VST & NVIT habitats.

DOC_Flx23ann = PULSE(DOC_Flx23yr,365,365)

DOCUMENT: Integrated Annual DOC Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

LPOC_Flx12yr(t) = LPOC_Flx12yr(t - dt) + (LPOC_Flx12b - LPOC_Flx12ann) * dt

INIT LPOC_Flx12yr = 0.0

DOCUMENT: Annual LPOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

LPOC_Flx12b = LPOC2_Flx12

DOCUMENT: LPOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of LPOC between the VST & NVIT habitats.

$LPOC_Flx12ann = PULSE(LPOC_Flx12yr, 365, 365)$

DOCUMENT: Integrated Annual POC Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$LPOC_Flx23yr(t) = LPOC_Flx23yr(t - dt) + (LPOC_Flx23b - LPOC_Flx23ann) * dt$

INIT $LPOC_Flx23yr = 0.0$

DOCUMENT: Annual LPOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$LPOC_Flx23b = LPOC2_Flx23$

DOCUMENT: LPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of LPOC between the VST & NVIT habitats.

$LPOC_Flx23ann = PULSE(LPOC_Flx23yr, 365, 365)$

DOCUMENT: Integrated Annual POC Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP_Flx12yr(t) = OP_Flx12yr(t - dt) + (OP_Flx12b - OP_Flx12ann) * dt$

INIT $OP_Flx12yr = 0.0$

DOCUMENT: Annual OP Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP_Flx12b = OP2_Flx12$

DOCUMENT: Other Plankton Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of OP between the NVST & VST habitats.

$OP_Flx12ann = PULSE(OP_Flx12yr, 365, 365)$

DOCUMENT: Integrated Annual OP Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP_Flx23yr(t) = OP_Flx23yr(t - dt) + (OP_Flx23b - OP_Flx23ann) * dt$

INIT $OP_Flx23yr = 0.0$

DOCUMENT: Annual OP Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP_Flx23b = OP2_Flx23$

DOCUMENT: Other Plankton Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of OP between the VST & NVIT habitats.

$OP_Flx23ann = PULSE(OP_Flx23yr, 365, 365)$

DOCUMENT: Integrated Annual OP Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$RPOC_Flx12yr(t) = RPOC_Flx12yr(t - dt) + (RPOC_Flx12b - RPOC_Flx12ann) * dt$

INIT $RPOC_Flx12yr = 0.0$

DOCUMENT: Annual RPOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$RPOC_Flx12b = RPOC2_Flx12$

DOCUMENT: RPOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of RPOC between the NVST & VST habitats.

RPOC_Flx12ann = PULSE(RPOC_Flx12yr,365,365)

DOCUMENT: Integrated Annual POC Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

RPOC_Flx23yr(t) = RPOC_Flx23yr(t - dt) + (RPOC_Flx23b - RPOC_Flx23ann) * dt

INIT RPOC_Flx23yr = 0.0

DOCUMENT: Annual RPOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

RPOC_Flx23b = RPOC2_Flx23

DOCUMENT: RPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of RPOC between the VST & NVIT habitats.

RPOC_Flx23ann = PULSE(RPOC_Flx23yr,365,365)

DOCUMENT: Integrated Annual POC Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

VST DOC & POC

VSTD0C(t) = VSTD0C(t - dt) + (DOC2prod + DOC2_Flx12 + DOC2_SedFlx - DOC2remin - DOC2_Flx23) * dt

INIT VSTD0C = 3966413

DOCUMENT: DOC 2, VST. (gC). Total DOC from Betty's Eshore data = 3.5 gC/m3. VST vol = 1133261 m3. INIT = 3966413 gC

DOC2prod = TotDOC2

DOCUMENT: Total DOC 2 Production, VST (gC/d).

DOC2_Flx12 = DOC_TE12

DOCUMENT: DOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of DOC between the NVST & VST habitats.

DOC2_SedFlx = 0.0*(IF(PARo>0.0) THEN(VSTwetar*MrshFlxDOC) ELSE(0.0))

DOCUMENT: DOC 2 Sediment Water Flux, VST. (gC/d). This is the mass exchange between the sediment and water.

DOC2remin = KDOC*ReminTC*(1-FRDOC)*VSTD0C

DOCUMENT: DOC 2 Remineralization, VST. (gC/d). A function of the DOC, the remineralization term, and a remin. constant. Cerco & Cole, 1994.

DOC2_Flx23 = DOC_TE23

DOCUMENT: DOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of DOC between the VST & NVIT habitats.

VSTLPOC(t) = VSTLPOC(t - dt) + (LPOC2prod + LPOC2_Flx12 - LPOC2hydrol - LPOC2_Flx23 - LPOC2_Set) * dt

INIT VSTLPOC = 1558233

DOCUMENT: Labile POC 2, VST. (gC). Shoal Run AFDW winter = 2.5 gC/m3, Assume labile fraction = 0.55. 1133261 m3. INIT = 1558233 gC.

$LPOC2_{prod} = LPOC2$

DOCUMENT: Labile POC 3, NVIT. (gC/d). The total POC production * labile fraction (55% Cerco&Cole).

$LPOC2_{Flx12} = LPOC_TE12$

DOCUMENT: LPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of LPOC between the VST & NVIT habitats.

$LPOC2_{hydrol} = KLPOC * HydrolTC * VSTLPOC$

DOCUMENT: LPOC 2 Hydrolysis, VST. (gC/d). A function of the POC, the hydrolysis term, and a constant. Cerco & Cole, 1994.

$LPOC2_{Flx23} = LPOC_TE34$

DOCUMENT: LPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of LPOC between the VST & NVIT habitats.

$LPOC2_{Set} = VSTLPOC * DetrSetlV/hVST$

DOCUMENT: LPOC 2 Settling, VST. (gC/d). This is the fraction of the water column LPOC pool that settles daily.

$VSTRPOC(t) = VSTRPOC(t - dt) + (RPOC2_{prod} + RPOC2_{Flx12} - RPOC2_{hydrol} - RPOC2_{Flx23} - RPOC2_{Set}) * dt$

INIT VSTRPOC = 1274918

DOCUMENT: Refractory POC 2, VST. (gC). Shoal Run AFDW winter = 2.5 gC/m³. Assume labile fraction = 0.45. 1133261 m³. INIT = 1274918 gC.

$RPOC2_{prod} = RPOC2$

DOCUMENT: Refractory POC 2, VST. (gC/d). The total POC production * refractory fraction (45% Cerco&Cole).

$RPOC2_{Flx12} = RPOC_TE12$

DOCUMENT: RPOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of RPOC between the NVST & VST habitats.

$RPOC2_{hydrol} = KRPOC * HydrolTC * VSTRPOC$

DOCUMENT: RPOC 2 Hydrolysis, VST. (gC/d). A function of the RPOC, the hydrolysis term, and a constant. Cerco & Cole, 1994.

$RPOC2_{Flx23} = RPOC_TE23$

DOCUMENT: RPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of RPOC between the VST & NVIT habitats.

$RPOC2_{Set} = VSTRPOC * DetrSetlV/hVST$

DOCUMENT: RPOC 2 Settling, VST. (gC/d). This is the fraction of the water column RPOC pool that settles daily.

$DOC2c = VSTD DOC/VSTvol$

DOCUMENT: DOC Concentration 2, VST. (gC/m³).

$DOC_TE12 = IF(FLorEB > 0) THEN (dVol2 * NVSTD DOC) ELSE$
 $IF(FLorEB < 0) THEN (dVol2 * DOC2c)$

ELSE (0.0)

DOCUMENT: DOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of DOC between the NVST & VST habitats.

DOC_TE23 = IF(FLorEB > 0) THEN (dVol3 * DOC2c) ELSE

IF(FLorEB < 0) THEN (dVol3 * NVITDOC)

ELSE (0.0)

DOCUMENT: DOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of DOC between the VST & NVIT habitats.

LPOC2 = FLPOC*TPOCprod2

DOCUMENT: Labile POC 3, NVIT. (gC/d). The total POC production * labile fraction (55% Cerco&Cole).

LPOC2c = VSTLPOC/VSTvol

DOCUMENT: LPOC Concentration 2, VST. (gC/m3).

LPOC_TE34 = IF(FLorEB > 0) THEN (dVol3 * LPOC2c) ELSE

IF(FLorEB < 0) THEN (dVol3 * NVITLPOCc)

ELSE (0.0)

DOCUMENT: LPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of LPOC between the VST & NVIT habitats.

LPOC__TE12 = IF(FLorEB > 0) THEN (dVol2 * NVSTLPOCc) ELSE

IF (FLorEB < 0) THEN (dVol2 * LPOC2c)

ELSE (0.0)

DOCUMENT: LPOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of LPOC between the NVST & VST habitats.

PhyPOCf = 0.80

DOCUMENT: Phytoplankton POC Fraction. (unitless). The fraction of total phyto POC loss that goes into the water column POC pool. Probably should be lower than 80% because most goes to grazing?

PhyTMort = Dia2_Mort+OP2Mort

DOCUMENT: Phytoplankton Total Mort. (gC/d).

RPOC2 = FRPOC*TPOCprod2

DOCUMENT: Refractory POC 3, NVIT. (gC/d). The total POC production * refractory fraction (45% Cerco&Cole).

RPOC2c = VSTRPOC/VSTvol

DOCUMENT: RPOC Concentration 2, VST. (gC/m3).

RPOC_TE23 = IF(FLorEB > 0) THEN (dVol3 * RPOC2c) ELSE

IF(FLorEB < 0) THEN (dVol3 * NVITRPOCc)

ELSE (0.0)

DOCUMENT: RPOC Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of RPOC between the VST & NVIT habitats.

$RPOC_TE12 = IF(FLorEB > 0) THEN (dVol2 * NVSTRPOCc) ELSE$
 $IF (FLorEB < 0) THEN (dVol2 * RPOC2c)$
 $ELSE (0.0)$

DOCUMENT: RPOC Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of RPOC between the NVST & VST habitats.

$TotDOC2 = Dia2_Exu + LPOC2hydrol + OP2Exu + RPOC2hydrol$

DOCUMENT: Total DOC Production. NVIT (gC/d).

$TPOC2c = LPOC2c + RPOC2c$

$TPOCprod2 = (PhyTMort * PhyPOCf) + (VSTwetar * SM2resus)$

DOCUMENT: Total Water Column POC Production Habitat 2, VST. (gC/d). The sum of diatoms, other plankton, sediment microalgae, and Zostera shoots.

PLANKTON CONTROL

$BMRd = 0.01$

DOCUMENT: Diatom Respiration Factor. (/d). From WES Ches. Bay model. 0.01/d or 0.003/d (Jan-May in salt water only).

$BMRop = 0.01$

DOCUMENT: OP Respiration Factor. (/d). From WES Ches. Bay model. 0.01/d.

$Chl2 = 1000 * (Dia2c + OP2c) / WCDia_Cchl$

DOCUMENT: Chlorophyll Conc. 2, VST. (mg/m³). This is the total phytoplankton mass converted to concentration and then to chlorophyll biomass using C:Chla=50.

$DiaExuk = 0.3$

DOCUMENT: Diatom Exudation Constant. 10% of Production is lost through exudation of DOC. 15% given in Moloney&Field 1991.

$DiaPT1 = 0.004$

DOCUMENT: Diatom Photosynthesis Temp Coeff. 1. (/degc²). Used in exp. curve.

$DiaPT2 = 0.006$

DOCUMENT: Diatom Photosynthesis Temp Coeff. 2. (/degc²). Used in exp. curve.

$DiaSedk = 0.25$

DOCUMENT: Diatom Sedimentation Coefficient. (m/d). Park & Kuo used 0.35 (Jan-May) and 0.1 (June-Dec).

$Dia_CN_wt = 5.7$

DOCUMENT: Diatome C:N Redfield Weight Ratio. 106:16 in weight units.

$Dia_Ik = 140$

DOCUMENT: Diatom Ik. (uE/m²/s). From Pax Shallow.

$Dia_Kdin = 10 \{uM\} DIN$

DOCUMENT: Diatom Ks DIN. The half sat. constant for DIN uptake by diatoms.

$Dia_MortvT = PRRd * EXP(KtBd * (WatTemp - Dia_RTopt))$

DOCUMENT: Diatom Mortality Temperature Control. (/d). This is the effect of temperature on diatom mortality.

Dia_Pmax = 1.0 {HPEL dia_Pmax=0.75; WES's Pd=2.25}

DOCUMENT: Diatom Pmax. (gC/gC/d).

Dia_PT_{opt} = 20

DOCUMENT: Diatom Photosynthesis Optimal Temperature. (degC). Like most everything else, estimated @ 20. Reduced to 15 to better represent the spring freshet.

Dia_PT_Ctrl = IF (WatTemp<=Dia_PT_{opt}) THEN
(EXP(-DiaPT1*(WatTemp-Dia_PT_{opt})^2)) ELSE
(EXP(-DiaPT2*(Dia_PT_{opt}-WatTemp)^2))

DOCUMENT: Diatom Photosynthesis Temperature Control. (). This is the effect of temperature on diatom photosynthesis.

Dia_RT_{opt} = 20

DOCUMENT: Diatom Respiration Optimal Temperature. (degC).

Dia_RT_Ctrl = BMRd*EXP(KtBd*(WatTemp-Dia_RT_{opt}))

DOCUMENT: Diatom Respiration Temperature Control. (/d). This is the effect of temperature on diatom respiration.

KtBd = 0.069

DOCUMENT: Diatom Respiration Temp Coeff. 1. (/degC). Used in exp. curve. From WES Ches. Bay model.

KtBop = 0.069

DOCUMENT: Other Plankton Photosynthesis Temp Coeff. 1. (/degC). Used in exp. curve.

OPE_{ex} = 0.3

DOCUMENT: Diatom Exudation Constant. 10% of Production is lost through exudation of DOC. 15% given in Moloney&Field 1991.

OPS_{ed} = 0.1

DOCUMENT: Diatom Sedimentation Coefficient. (m/d). Park & Kuo used 0.1 m/d.

OP_CN_{wt} = 5.7

DOCUMENT: Other Plankton C:N Redfield Weight Ratio. 106:16 in weight units.

OP_{lk} = 140

DOCUMENT: Other Plankton lk. (uE/m²/s). From Pax Shallow.

OP_{K_d} = 10 {uM DIN}

DOCUMENT: Other Plankton K_s DIN. The half sat. constant for DIN uptake by OP.

OP_{MortvT} = PRR_{op}*EXP(KtBop*(WatTemp-OP_RT_{opt}))

DOCUMENT: Other Plankton Mortality Temperature Control. (/d). This is the effect of temperature on other plankton mortality.

OP_Pmax = 1.0 {g C/g C/day; WES's Green algal Pg=2.5}

DOCUMENT: Other Plankton Pmax. (gC/gC/d).

OP_PT1 = 0.008

and respiration.

$ZEpiC24hr = PULSE(ZEpiCday, 2, 1)$

DOCUMENT: Integrated Daily Zostera Epiphyte Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZEpiCyr(t) = ZEpiCyr(t - dt) + (ZEpiNetC3 - ZEpiCann) * dt$

INIT $ZEpiCyr = 0.0$

DOCUMENT: Annual Zostera Epiphyte Productivity. (gC/m²/yr) This accumulates (or loses?) net epiphyte each DT and spits out yearly values.

$ZEpiNetC3 = ZEpiNetC$

DOCUMENT: Zostera Epiphyte Net C Production. (gC/m²/d). Gross Prod - Respiration.

$ZEpiCann = PULSE(ZEpiCyr, 365, 365)$

DOCUMENT: Integrated Annual Zostera Epiphyte Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZRRnetCday(t) = ZRRnetCday(t - dt) + (ZRRnet2 - ZRRnetC24) * dt$

INIT $ZRRnetCday = 0$

DOCUMENT: Daily Zostera RR Productivity. (gC/m²) This accumulates (or loses?) net RR each DT and spits out daily values.

$ZRRnet2 = ZRRnetC$

DOCUMENT: Zostera RR Net Carbon Production. (gC/m²/d). The sum of translocation, RR respiration, RR mortality, and RR C lost to bed storage.

$ZRRnetC24 = PULSE(ZRRnetCday, 24, 24)$

DOCUMENT: Integrated Daily Zostera RR Net Production. (gC/m²/d). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZRRnetCyr(t) = ZRRnetCyr(t - dt) + (ZRRnet3 - ZRRnetCann) * dt$

INIT $ZRRnetCyr = 0$

DOCUMENT: Annual Zostera RR Productivity. (gC/m²) This accumulates (or loses?) net RR each DT and spits out annual values.

$ZRRnet3 = ZRRnetC$

DOCUMENT: Zostera RR Net Carbon Production. (gC/m²/d). The sum of translocation, RR respiration, RR mortality, and RR C lost to bed storage.

$ZRRnetCann = PULSE(ZRRnetCyr, 365, 365)$

DOCUMENT: Integrated Yearly Zostera RR Net Production. (gC/m²/d). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZRRnetNyr(t) = ZRRnetNyr(t - dt) + (ZRRNdem2 - ZRRNdemAnn) * dt$

INIT $ZRRnetNyr = 0$

DOCUMENT: Annual Zostera RR N Productivity. (gN/m²) This accumulates (or loses?) net RR each DT and spits out annual values.

$ZRRNdem2 = ZRRNdemand$

DOCUMENT: Zostera RR Net Nitrogen Production. (gN/m²/d).

$ZRRNdemAnn = PULSE(ZRRnetNyr, 365, 365)$

DOCUMENT: Integrated Yearly Zostera RR Net Production. (gN/m²/d). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZRRNuptyr(t) = ZRRNuptyr(t - dt) + (ZRRNupt2 - ZRRNuptAnn) * dt$

INIT $ZRRNuptyr = 0$

DOCUMENT: Annual Zostera RR N Uptaken. (gN/m²) This accumulates (or loses?) net RR each DT and spits out annual values.

$ZRRNupt2 = ZRRNupt$

DOCUMENT: Zostera RR Nitrogen Uptake. (gN/m²/d).

$ZRRNuptAnn = PULSE(ZRRNuptyr, 365, 365)$

DOCUMENT: Integrated Yearly Zostera RR Nitrogen Uptake. (gN/m²/d). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZSHCday(t) = ZSHCday(t - dt) + (ZSHCnet2 - ZSHC24hr) * dt$

INIT $ZSHCday = 0.0$

DOCUMENT: Daily Zostera Shoot Productivity. (gC/m²) This accumulates (or loses?) net zostera productivity each DT and spits out daily values.

$ZSHCnet2 = ZSHCnet$

DOCUMENT: Zostera Shoot Net Carbon Production. (gC/m²/d). This is difference between gross P and respiration.

$ZSHC24hr = PULSE(ZSHCday, 2, 1)$

DOCUMENT: Integrated Daily Zostera Shoot Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZSHCyr(t) = ZSHCyr(t - dt) + (ZSHCnet3 - ZSHCAnn) * dt$

INIT $ZSHCyr = 0.0$

DOCUMENT: Annual Zostera Shoot Productivity. (gC/m²) This accumulates (or loses?) net Z Shoot Prod each DT and spits out yearly values.

$ZSHCnet3 = ZSHCnet$

DOCUMENT: Zostera Shoot Net Carbon Production. (gC/m²/d). This is difference between gross P and respiration.

$ZSHCAnn = PULSE(ZSHCyr, 365, 365)$

DOCUMENT: Integrated Annual Zostera Shoot Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZSHNdemyr(t) = ZSHNdemyr(t - dt) + (ZSHNdem2 - ZSHNdemAnn) * dt$

INIT $ZSHNdemyr = 0.0$

DOCUMENT: Annual Zostera Shoot Productivity. (gN/m²) This accumulates (or loses?) net Z Shoot Prod each DT and spits out yearly values.

$ZSHNdem2 = ZSHNdemand$

DOCUMENT: Zostera Shoot Net Nitrogen Production. (gN/m²/d). This is difference between gross P and respiration.

$ZSHNdemAnn = PULSE(ZSHNdemyr, 365, 365)$

DOCUMENT: Integrated Annual Zostera Shoot Net Nitrogen Production. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZSHNuptyr(t) = ZSHNuptyr(t - dt) + (ZSHNupt2 - ZSHNuptAnn) * dt$

INIT ZSHNuptyr = 0.0

DOCUMENT: Annual Zostera Shoot N Uptaken. (gN/m²) This accumulates (or loses?) net Z Shoot Prod each DT and spits out yearly values.

$ZSHNupt2 = ZSHNupt$

DOCUMENT: Zostera Shoot Net Nitrogen Uptake. (gN/m²/d).

$ZSHNuptAnn = PULSE(ZSHNuptyr, 365, 365)$

DOCUMENT: Integrated Annual Zostera Shoot Nitrogen Uptake. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$ZepiCdaytot = ZepiC24hr * VSTwetar$

DOCUMENT: Zostera epi C daily total net. (gC/d). The areal rate * the habitat area.

$ZepiCyrctot = ZepiCann * VSTwetar$

DOCUMENT: Zostera epi C annual total net. (gC/yr). The areal rate * the habitat area.

$ZEpiNetC = ZEpiProd - ZEpiResp$

DOCUMENT: Zostera Epiphyte Net C Production. (gC/m²/d). Gross Prod - Respiration.

$ZRRCdaytot = ZRRnetC24 * VSTwetar$

DOCUMENT: Zostera RR C daily total net. (gC/d). The areal rate * the habitat area.

$ZRRCyrctot = ZRRnetCann * VSTwetar$

DOCUMENT: Zostera RR C annual total net. (gC/yr). The areal rate * the habitat area.

$ZRRnetC = ZCtrans - ZRRresp$

DOCUMENT: Zostera RR Net Carbon Production. (gC/m²/d). The difference between translocation and RR respiration.

$ZSHCdaytot = ZSHC24hr * VSTwetar$

DOCUMENT: Zostera Shoot C daily total net. (gC/d). The areal rate * the habitat area.

$ZSHCyrctot = ZSHCAnn * VSTwetar$

DOCUMENT: Zostera Shoot C annual total net. (gC/yr). The areal rate * the habitat area.

PAR, TEMP, DEPTH

$Declination = 0.39637 - 22.9133 * \cos(\psi) + 4.02543 * \sin(\psi) - 0.3872 * \cos(2 * \psi) + 0.052 * \sin(2 * \psi)$

DOCUMENT: Solar declination. Used to define photoperiod for a given day and latitude. Kirk, 1994, p. 35. Psi is in radians.

$\Delta WL = tidal_wl - DELAY(tidal_wl, DT)$

DOCUMENT: d Tidal Water Level. (m). This is the change in tidal wl over dt. DELAY delays the output of a value by a given time lag.

dVol2 = deltaWL*(VSTwetar+NVITwetar+VITwetar)

DOCUMENT: delta Volume 2, VST. (m3). This calculates the change in volume each time step.

DELAY delays the output of a value by a given time lag.

dVol3 = deltaWL*(NVITwetar+VITwetar)

DOCUMENT: delta Volume 3, NVIT. (m3). This calculates the change in volume each time step.

DELAY delays the output of a value by a given time lag.

eps = 0.00 {"Near-Zero"}

DOCUMENT: eps. (m). I have no idea what eps stands for but it is a potential correction factor for deltaWL.

FLorEB = IF (deltaWL-eps > 0.0) THEN 1 ELSE IF (deltaWL-eps < 0.0) THEN -1 ELSE 0

DOCUMENT: Flood or Ebb. This switch determines if the tidal WL is increasing or decreasing.

GloPtM2 = MSL+(0.363*COS(0.5059*modlhrs-4.365))

GIPTM2S2 = MSL+(0.363*COS(0.5059*modlhrs-4.365))+(0.067*COS(0.5236*modlhrs-5.0388))

DOCUMENT: Tidal water level. (m). This is total tide height from a combination of mean sea level and the first 2 harmonic components (M2 and S2) of the tidal equation for Gloucester Point, VA . Tide equation relative to Mean Low Water!

GIPTid93 = MSL+(0.356*COS(0.5059*modlhrs-1.583))+(0.067*COS(0.5236*modlhrs-5.0388))+(0.074*COS(0.4964*modlhrs+1.2636))+(0.047*COS(0.2625*modlhrs-1.8535))+(0.037*COS(0.2434*modlhrs+0.0332))

DOCUMENT: Tidal water level. (m). This is total tide height from a combination of mean sea level and the first 5 harmonic components of the tidal equation for Gloucester Point, VA, tidal year 1993 . Tide equation relative to Mean Low Water!

GIPTid95 = MSL+(0.363*COS(0.5059*modlhrs-4.365))+(0.067*COS(0.5236*modlhrs-5.0388))+(0.075*COS(0.4964*modlhrs+1.6685))+(0.044*COS(0.2625*modlhrs-1.9199))+(0.092*COS(0.0014*modlhrs+2.2811))+(0.098*COS(0.0007*modlhrs+2.0071))

DOCUMENT: Tidal water level. (m). This is total tide height from a combination of mean sea level and the first 6 harmonic components of the tidal equation for Gloucester Point, VA, Tidal year 1995 . Tide equation relative to Mean Low Water!

hfilm = 0.01

DOCUMENT: h film. (m). The thickness of the water layer over the intertidal habitats that is not exchanged. Used to prevent habitats from being totally dry.

hNVIT = IF(tidal_wl>-0.36)THEN(tidal_wl-zNVIT)ELSE(0)

DOCUMENT: NVIT Habitat depth. (m). This is the depth of the nonvegetated intertidal habitat 3 over the tidal cycle. The IF..THEN..ELSE is to assure that depth is never negative.

hNVST = tidal_wl-zNVST

DOCUMENT: NVST Habitat depth. (m). This is the depth of the nonvegetated subtidal habitat 1 over the tidal cycle.

hVIT = IF(tidal_wl>0.0)THEN(tidal_wl-zVIT)ELSE(0.0)

DOCUMENT: VIT Habitat depth. (m). This is the depth of the vegetated intertidal habitat 4 over the tidal cycle. The IF..THEN..ELSE is to assure that depth is never negative.

$hVST = tidal_wl - zVST$

DOCUMENT: VST Habitat depth. (m). This is the depth of the vegetated subtidal habitat 2 over the tidal cycle.

$Insolation = 28.25 - 16.75 * \cos(2 * \pi * (JD + 10) / 365)$

DOCUMENT: Incident solar irradiance (insolation) at Gloucester Point, VA in Einsteins/m²/day. Taken from Wetzel and Neckles (1986).

$JD = \text{IF } Steady=0 \text{ THEN } JDstart + \text{INT}(TIME) \text{ ELSE } JDstart$

DOCUMENT: Julian Day. TIME is days but the integer is used to prevent rounding errors.

$JDstart = 0$

DOCUMENT: Julian Day to start. User can input starting day, otherwise model starts 1 January.

$latitude = 38 * (\pi / 180)$

DOCUMENT: Latitude. (radians). User can input latitude in degrees, converted to radians. Lower Ches. Bay assumed to be 38N.

$MaxIrradiance = 277.78 * \pi * Insolation / (2 * photoperiod)$

DOCUMENT: Maximum Daily Irradiance. (uEinsteins/m²/sec). This converter calculates the maximum daily irradiance value from the total daily insolation.

$modlhrs = TIME * 24$

$MSL = 0.00$

DOCUMENT: Mean Sea Level. (m). This is h₀ in the tidal equation and sets reference baseline for all elevations.

$NVIT_{Amax} = 1.0E+6$

DOCUMENT: Maximum area of NVIT. (m²). This sets maximum area for habitat 3 when marsh is fully inundated.

$NVIT_{fwetA} = NVIT_{wetar} / NVIT_{Amax}$

DOCUMENT: NVIT Fractional Wet Area. (unitless ratio). This is the fraction NVIT wet area is of the max. wet area.

$NVIT_{vol} = \text{MAX}(h_{NVIT} - h_{film}, 0.0) * NVIT_{wetar}$

DOCUMENT: Volume of NVIT. (m³). This is the volume of the nonvegetated intertidal habitat 2 based upon the wet area * the habitat depth relative to msl and a fluctuating free surface. H_{film} maintains some water over the marsh surface.

$NVIT_{wetar} = \text{IF } (tidal_wl > -0.36) \text{ AND } (tidal_wl < 0.0) \text{ THEN } (GIIntWetArea)$

$\text{ELSE IF } (tidal_wl \geq 0.0) \text{ THEN } NVIT_{Amax}$

$\text{ELSE } (0.0)$

DOCUMENT: Inundated area of NVIT. (m²). This is the inundated area of the nonvegetated intertidal habitat 3 that ranges from -0.36 m and 0.0m relative to MSL.

$NVST_{vol} = h_{NVST} * NVST_{wetar}$

DOCUMENT: Volume of NVST. (m³). This is the volume of the nonvegetated subtidal habitat 1 based upon the wet area X the habitat depth relative to msl and a fluctuating free surface.

$NVST_{wetar} = 4200000$

DOCUMENT: Inundated Area of NVST. (m²). This is the total wetted area for the nonvegetated subtidal

habitat 1. This value is assumed to be constant.

$PAR_o = \text{MAX}(\text{MaxIrradiance} * \text{COS}(2 * \text{PI} * (\text{thours} - 12) / (2 * \text{photoperiod})), 0.0)$

DOCUMENT: Surface Downwelling PAR. ($\mu\text{E}/\text{m}^2/\text{s}$). This is an hourly light curve formulated similar as that in Wetzel and Neckles (1986).

$\text{photoperiod} = 11.75 - 2.25 * \text{COS}(2 * \text{PI} * (\text{JD} + 10) / 365)$

DOCUMENT: Photoperiod function taken from Wetzel and Neckles (1986). Calculates photoperiod in hours/day.

$\text{psi} = \text{MOD}(\text{JD} - 1.365) / 365 * 2 * \text{PI}$

DOCUMENT: psi. (radians). Date of year expressed as an angle that provides the argument, in radians, for solar declination formula. $\text{MDAY} = \text{Model day}$, starting at day 1 on Jan 1. Kirk, 1983, p. 36.

$\text{sinB} = \text{SIN}(\text{latitude}) * \text{SIN}(\text{Declination} * \text{PI} / 180) - \text{COS}(\text{latitude}) * \text{COS}(\text{Declination} * \text{PI} / 180) * \text{COS}(\text{tau})$

DOCUMENT: sin B. (unitless). Solar elevation (solar angle) calculated according to JTO Kirk. For use in light attenuation due to plant biomass.

$\text{Steady} = 0 \text{ } \{0/1: \text{annual cycle or fixed day}\}$

$\text{tau} = \text{thours} / 24 * 2 * \text{PI}$

DOCUMENT: Tau. (radians). Clock hour in degrees, converted to radians. From JTO Kirk.

$\text{thours} = \text{MOD}(\text{TIME}, 1) * 24$

DOCUMENT: Time in hours. This converter takes time in days and converts it to hours for use in physical forcing functions (i.e. tidal wl and PAR).

$\text{tidal_wl} = \text{GIPTid93}$

DOCUMENT: Tidal water level. (m). This is total tide height from either the M2 only, the M2S2, or the top 6 components of the tidal equation for Gloucester Point, VA in 1993 or 1995. Tide equation relative to Mean Low Water!

$\text{VIT}_{\text{Amax}} = 850000$

DOCUMENT: Maximum area of VIT. (m^2). Used in the calculation of sediment biogeochemical stocks.

$\text{VIT}_{\text{fwetA}} = \text{VIT}_{\text{wetar}} / \text{VIT}_{\text{Amax}}$

DOCUMENT: VIT Fractional Wet Area. (unitless ratio). This is the fraction VIT wet area is of the max. wet area.

$\text{VIT}_{\text{vol}} = \text{MAX}(\text{hVIT} - \text{hfilm}, 0.0) * \text{VIT}_{\text{wetar}}$

DOCUMENT: Volume of VIT. (m^3). This is the volume of the vegetated intertidal habitat 2 based upon the wet area * the habitat depth relative to msl and a fluctuating free surface. Hfilm maintains some water over the marsh surface.

$\text{VIT}_{\text{wetar}} = \text{IF}(\text{tidal_wl} \geq 0.0) \text{ AND } (\text{tidal_wl} < 0.36)$

$\text{THEN } (\text{GIIntWetArea} - \text{NVIT}_{\text{Amax}}) \text{ ELSE IF}(\text{tidal_wl} > 0.36)$

$\text{THEN } (\text{VIT}_{\text{Amax}}) \text{ ELSE } (0.0)$

DOCUMENT: Inundated area of VIT. (m^2). This is the wetted area of the vegetated intertidal habitat 4. This value fluctuates with tidal water level.

$\text{VST}_{\text{sedVol}} = \text{VST}_{\text{wetar}} * 0.1$

DOCUMENT: Veg. Subtidal Sediment Volume. (m^3). The wetarea (m^2) * sediment depth (m).

$$VSTvol = hVST * VSTwetar$$

DOCUMENT: Volume of VST. (m3). This is the volume of the vegetated subtidal habitat 2 based upon the wet area * the habitat depth relative to msl and a fluctuating free surface.

$$VSTwetar = 1200000$$

DOCUMENT: Inundated area of VST. (m2). This is the wetted area of the vegetated subtidal habitat 2. This value is assumed to be constant.

$$WatTemp = 16.25 - 13.75 * \cos(2 * \pi * (JD - 25) / 365)$$

DOCUMENT: Water Temperature. (degC). This is a water temperature function for the York River, V.A. Taken from Wetzel and Neckles (1986).

$$zNVIT = -0.36$$

DOCUMENT: Elevation of the NVIT habitat 3. (m). This is the reference elevation for the nonvegetated intertidal habitat 3 relative to MSL. The average elevation for this habitat recorded at the GI using GPS = -0.526 m.

$$zNVST = -1.88$$

DOCUMENT: Elevation of NVST habitat 1. (m). This is the reference elevation for the nonvegetated subtidal habitat relative to MSL. Calculated as the average elevation.

$$zVIT = 0.0$$

DOCUMENT: Elevation of the VIT habitat 4. (m). This is the reference elevation for the vegetated intertidal habitat 4 relative to MSL. Calculated as the minimum for the habitat.

$$zVST = -0.881$$

DOCUMENT: Elevation of VST habitat 2. (m). This is the reference elevation for the vegetated subtidal habitat 2 relative to MSL. Calculated as the average elevation.

$$GIIntWetArea = \text{GRAPH}(\text{tidal_wl})$$

(-0.36, 0.00), (-0.309, 83000), (-0.257, 160000), (-0.206, 330000), (-0.154, 500000), (-0.103, 660000), (-0.0514, 830000), (4.16e-17, 1e+06), (0.0514, 1.2e+06), (0.103, 1.3e+06), (0.154, 1.4e+06), (0.206, 1.5e+06), (0.257, 1.6e+06), (0.309, 1.7e+06), (0.36, 1.8e+06)

DOCUMENT: GI Intertidal Wet Area. This is the intertidal wetted area (m2) derived using a drawn HC with a sigmoid shape. Tide ranges from 0-0.4 m and area ranges from 0 to 1E+06 m2.

VST LIGHT

$$aZm = 0.002$$

DOCUMENT: Attenuation due to Zostera. (m2/gC). Canopy light extinction measured by Morris (1989) to be 0.002 and borrowed from Pinkney & Zingmark 1993. This value was determined experimentally for *Spartina alterniflora* and used for eelgrass.

$$DOCatn = 0.14$$

DOCUMENT: PAR attenuation due to dissolved organic matter. (m2/gC). McPherson & Miller (1987). I estimated this assuming 21% attenuation due to DOC, a 1.5 gC/m3 DOC Conc., and a target Ktotal = 1.0. I hope this works.....

$$EpiAtten = \sqrt{\text{MAX}(ZEpiLeaf_Ratio - 0.1, 0.0) / 2.9}$$

DOCUMENT: Epiphyte-induced light attenuation at Zostera shoot surface (fractional reduction). Wetzel & Neckles:

$0.5 * (1.0 - \text{MAX}(1.0 - \text{SQRT}(\text{MAX}(\text{ZEpiLeaf_Ratio} - 0.1, 0) / (3.0 - 0.1)), 0.0))$

$\text{KdDOC} = \text{DOC2c} * \text{DOCatn}$

$\text{Kdphy} = \text{Chl2} * \text{Phytatn}$

$\text{KdPOC} = \text{POCatn} * \text{TPOC2c}$

$\text{Kdwater} = 0.04$

DOCUMENT: PAR K attenuation due to water. (/m). From Kirk and McPherson & Miller 1987

$\text{Kd_switch} = 2$

DOCUMENT: Kd switch. (unitless). Switch used to determine method of calculation for submarine light attenuation. 0=fixed, constant Kd, 1=data driven variable Kd, 2=compute Kd from individual factors.

$\text{Kttl} = \text{Kdwater} + \text{Kdphy} + \text{KdDOC} + \text{KdPOC}$

DOCUMENT: VST total K attenuation. (/m).

$\text{PARZleaf} = (1.0 - 0.75 * \text{EpiAttn}) * \text{VSTPAR}$

DOCUMENT: PAR at Zostera leaf. ($\mu\text{E}/\text{m}^2/\text{s}$). Formulated after WetNeck Grazer model.

$\text{pctEpiAttn} = \text{PARZleaf} / (\text{VSTPAR} + 1\text{E-}10)$

DOCUMENT: Percent Epiphyte Attenuation. (unitless). The percent decrease in submarine light due to epiphytes

$\text{Phytatn} = 0.0138$

DOCUMENT: PAR attenuation due to Phytoplankton. (m^2/mgChl). From McPherson & Miller (1987). 0.0138 m^2/mgchl .

$\text{POCatn} = 0.14$

DOCUMENT: PAR attenuation due to Particulate organic matter. (m^2/gC). McPherson & Miller (1987). I estimated this assuming 72% attenuation due to POC, 5 gC/m^3 DOC Conc., and a target $\text{Ktotal} = 1.0$. I hope this works.....

$\text{SM2PAR} = \text{IF}(\sin B > 0.0) \text{ THEN } (\text{VSTPAR}_2 * \text{EXP}(-aZm * \text{ZSHC} / \sin B)) \text{ ELSE } (0.0)$

DOCUMENT: Sediment Microalgae PAR, VST. ($\mu\text{E}/\text{m}^2/\text{s}$). This is the PAR that reaches the sediment surface in the VST after being attenuated by depth and Zostera biomass. Prob. will change when PAR attenuation due to phytoplankton is entered.

$\text{VSTKd} = \text{IF } \text{Kd_switch} = 0 \text{ THEN } 1.0 \text{ ELSE IF } \text{Kd_switch} = 1 \text{ THEN } 1.0 \text{ ELSE } \text{Kttl}$

DOCUMENT: Vegetated Subtidal Downwelling Attenuation Coefficient.

$\text{VSTPAR} = \text{PARo} * \text{EXP}(-\text{VSTKd} * 0.5 * h\text{VST})$

DOCUMENT: Vegetated Subtidal PAR. ($\mu\text{E}/\text{m}^2/\text{s}$). This is the depth variable submarine light based upon downwelling attenuation. The 0.5 is an attempt to predict light at mid-depth.

$\text{VSTPAR}_2 = \text{PARo} * \text{EXP}(-\text{VSTKd} * h\text{VST})$

DOCUMENT: Vegetated Subtidal PAR. ($\mu\text{E}/\text{m}^2/\text{s}$). This is the depth variable submarine light based upon downwelling attenuation. This predicts PAR at the bottom for use in microalgal photosynthesis.

VST DIATOMS

$$\text{Dia2}(t) = \text{Dia2}(t - dt) + (\text{Dia2_PNS} + \text{Dia2_Flx12} - \text{Dia2_Exu} - \text{Dia2_Sed} - \text{Dia2_Resp} - \text{Dia2_Mort} - \text{Dia2_Flx23}) * dt$$

INIT Dia2 = 186988

DOCUMENT: Diatom 2 mass, VST. (gC). INIT = 10 mgChla/m3. Assume 50:1 C:Chl, fraction diatom = 0.33. INIT dia = 0.165 gC/m3, * 1133261 m3 = 186988 gC.

$$\text{Dia2_PNS} = \text{Dia2} * \text{Dia2Photo}$$

DOCUMENT: Diatom 2 Production, VST. (gC/d). From diatom photosynthesis and diatom biomass.

$$\text{Dia2_Flx12} = \text{Dia_TE12}$$

DOCUMENT: Diatom Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of diatoms between the NVST & VST habitats.

$$\text{Dia2_Exu} = \text{DiaExuk} * \text{Dia2_PNS}$$

DOCUMENT: Diatom 2 Exudation, VST. (gC/d). This is a fraction of diatom production.

$$\text{Dia2_Sed} = \text{DiaSedk} * \text{Dia2} / h\text{VST}$$

DOCUMENT: Diatom 2 Sedimentation, VST. (gC/d). This is loss to sedimentation from the sed coeff. and the diatom mass.

$$\text{Dia2_Resp} = \text{Dia2} * \text{Dia_RT_Ctrl}$$

DOCUMENT: Diatom 2 Respiration, VST. (gC/d).

$$\text{Dia2_Mort} = \text{Dia_MortvT} * \text{Dia2}$$

DOCUMENT: Diatom 2 Mortality, VST. (gC/d). This is loss to mortality from the mort. coeff. and the diatom mass.

$$\text{Dia2_Flx23} = \text{Dia_TE23}$$

DOCUMENT: Diatom Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of diatoms between the VST & NVIT habitats.

$$\text{Dia2c} = \text{Dia2} / \text{VSTvol}$$

DOCUMENT: Diatom Concentration 2, VST. (gC/m3). This is the diatom concentration in the VST habitat. Dia2 is in mass units.

$$\text{Dia2gNm2} = \text{Dia2Nremov} * 14 / 1000 / \text{VSTwetar}$$

DOCUMENT: Dia 2 N removal gN/m2/d.

$$\text{Dia2NetCar} = \text{Dia2NetCvol} * h\text{VST}$$

DOCUMENT: Dia2 Net C by area (gC/m2/d). The volumetric rate * the depth.

$$\text{Dia2NetCvol} = \text{Dia2_NetP} / \text{VSTvol}$$

DOCUMENT: Diatom 2 Net Production, NVIT. (gC/m3/d). This is volumetric net prod=grosP-resp.

$$\text{Dia2NetNar} = \text{Dia2NetCar} / \text{Dia_CN_wt}$$

DOCUMENT: Dia Net N demand by area (gC/m2/d). The volumetric rate * the depth.

$$\text{Dia2NetNvol} = \text{Dia2NetCvol} / \text{Dia_CN_wt}$$

DOCUMENT: Diatom Net N demand by volume. (gN/m³/d).

$\text{Dia2Nremov} = \text{Dia_Pmax} * \text{Dia2_NLim} * 1000 * \text{Dia2c} / 14 / \text{Dia_CN_wt} * \text{VSTvol}$

DOCUMENT: Diatom 2 Nitrogen Removal Equation (mmoleN/d).

$\text{NLim} * \text{Vmax} / \text{C:N} * \text{Biomass} / 14 * 1000 * \text{VSTvol}$ to convert from gN/gN/d to mmoleN/d.

$\text{Dia2Nuptake2} = \text{IF}(\text{PARo} > 0.0) \text{ THEN } (\text{Dia2Nremov}) \text{ ELSE } (0.0)$

$\text{Dia2Photo} = \text{Dia_Pmax} * \text{Dia_PT_Ctrl} * \text{Dia2_Glim}$

DOCUMENT: Diatom 3 Photosynthesis, NVIT. (gC/gC/d). This is the specific diatom photo. function.

$\text{Dia2_Glim} = \text{IF}(\text{PARo} > 0.0) \text{ THEN}$

$\text{IF}(\text{Dia2_NLim} > \text{Dia2_PvI}) \text{ THEN } (\text{Dia2_NLim}) \text{ ELSE } (\text{Dia2_PvI})$

$\text{ELSE } (0.0)$

DOCUMENT: Diatom 3 Growth Limitation, NVIT. (unitless) Chooses between light and nutrient limitation.

$\text{Dia2_NetP} = \text{Dia2_PNS} - \text{Dia2_Resp}$

DOCUMENT: Diatom 2 Net Production, VST. (gC/d). This is net prod=grosP-resp.

$\text{Dia2_NLim} = \text{WCDIN2c} / (\text{Dia_Kdin} + \text{WCDIN2c})$

DOCUMENT: Diatom 3 Nitrogen limitation, NVIT. (unitless). This the hyperbolic tangent curve.

$\text{Dia2_Nupt} = \text{IF}(\text{PARo} > 0.0) \text{ THEN } (\text{Dia2_NetP} / \text{Dia_CN_wt} * 1000 / 14)$

$\text{ELSE} (0.0)$

DOCUMENT: Diatom 2 Nitrogen Uptake, VST. (mmoleN/d). This is the net production (gC/d) converted to N using the Redfield C:N.

$\text{Dia2_PvI} = \text{VSTPAR} / (\text{Dia_Ik} + \text{VSTPAR})$

DOCUMENT: Diatom 2 Pvs I curve, VST. (unitless). The standard hyperbolic tangent curve.

$\text{Dia_TE12} = \text{IF}(\text{FLorEB} > 0) \text{ THEN } (\text{dVol2} * \text{NVSTDiaC}) \text{ ELSE}$

$\text{IF}(\text{FLorEB} < 0) \text{ THEN } (\text{dVol2} * \text{Dia2c})$

$\text{ELSE } (0.0)$

DOCUMENT: Diatom Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of diatoms between the NVST & VST habitats.

$\text{Dia_TE23} = \text{IF}(\text{FLorEB} > 0) \text{ THEN } (\text{dVol3} * \text{Dia2c}) \text{ ELSE}$

$\text{IF}(\text{FLorEB} < 0) \text{ THEN } (\text{dVol3} * \text{NVITDiaC})$

$\text{ELSE } (0.0)$

DOCUMENT: Diatom Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of diatoms between the VST & NVIT habitats.

VST NITROGEN

$\text{SDIN2}(t) = \text{SDIN2}(t - dt) + (\text{SDIN2prod} - \text{SDIN2los}) * dt$

INIT SDIN2 = 1.8e07

DOCUMENT: Sediment DIN 2, VST. (mmoles N). This value was derived from 150 uM = 150 mmol/m³. * 1,200,000 m² * 0.10 m (sed depth).

$SDIN2_{prod} = JanesReminRate * VST_{wet}ar$

DOCUMENT: Sediment DIN 2 Production, VST. (mmole/d). This is from a temperature dependent function and the sed DIN standing stock.

$SDIN2_{los} = 0$

DOCUMENT: Sediment DIN 2 Loss, VST. (mmole/d). The loss term for sediment DIN. From Zostera RR N uptake.

$WCDIN2(t) = WCDIN2(t - dt) + (WCDIN2_{prod} + DIN2_Flx12 + DIN2_SWflx - DIN2_{los} - DIN2_Flx23) * dt$

INIT $WCDIN2 = 12142082$

DOCUMENT: Water Column DIN, VST. (mmoles). This is initialized for the winter, lower Chesapeake Bay. INIT = 0.15 mg/L = 10.7 mmoles/m³. 10.7 mmoles/m³ * 1133261 m³ = 12,142,082 mmoles.

$WCDIN2_{prod} = DOC2remin/DOM_CN/14 * 1000$

DOCUMENT: Water Column DIN 2 production. (mmolesN/d). This is the water column remineralization term.

$DIN2_Flx12 = DIN_TE12$

DOCUMENT: DIN Tidal Exchange between Habitats 1 & 2. (mmoles/d). The physical exchange of DIN between the NVST and VST habitats.

$DIN2_SWflx = IF(PAR_0 > 0.0) THEN (SONE_DIN2 * VST_{wet}ar) ELSE (0.0)$

DOCUMENT: DIN 2 SONE flux. (mmol/d). Veg subtidal SONE flux * VST wet area to derive units. Flux is 0.0 at night (I have no data for dark rates).

$DIN2_{los} = Dia2Nuptake2 + OP2Nuptake2 + ZSHNupWC$

DOCUMENT: Water Column DIN 2 loss. (mmoles/d). This is the water column DIN loss term to N uptake by phototrophs.

$DIN2_Flx23 = DIN_TE23$

DOCUMENT: DIN Tidal Exchange between Habitats 2 & 3. (mmoles/d). The physical exchange of DIN between the VST and NVIT habitats.

$DIN_TE12 = IF(FLorEB > 0) THEN (dVol2 * NVSTDIN) ELSE$

$IF(FLorEB < 0) THEN (dVol2 * WCDIN2c)$

$ELSE (0.0)$

DOCUMENT: DIN Tidal Exchange between Habitats 1 & 2. (mmoles/d). The physical exchange of DIN between the NVST and VST habitats.

$DIN_TE23 = IF(FLorEB > 0) THEN (dVol3 * WCDIN2c) ELSE$

$IF(FLorEB < 0) THEN (dVol3 * NVITDIN)$

$ELSE (0.0)$

DOCUMENT: DIN Tidal Exchange between Habitats 2 & 3. (mmoles/d). The physical exchange of DIN between the VST and NVIT habitats.

$JanesReminRate = 25.85$

DOCUMENT: Jane Caffrey's Remineralization Rate. (mmol/m²/d). I calculated this value from Table 2 of Caffrey & Kemp (1990), this was 1077 μ molN/m²/h.

$SDIN2c = SDIN2/VSTsedVol$

DOCUMENT: Sediment DIN 2 Concentration, VST. (mmoles/m³). The mass (mmoles) over the sediment volume (m³).

$SDIN@30 = 0.00172$

DOCUMENT: Sediment DIN Remin. Rate @ 30degC. (gC/gC/d). This is the rate at the optimum temperature for use in an Arrhenius function.

$SDIN@30_2 = 0.00172$

DOCUMENT: Sediment DIN Remin. Rate @ 30degC. (gC/gC/d). This is the rate at the optimum temperature for use in an Arrhenius function.

$SDINfactor = 1.1$

DOCUMENT: Sediment DIN Remineralization Factor. This is the factor for use in the calculation of sed. DIN remin.

$SDINremin = SDIN@30 * SDINfactor^{(WatTemp-30)}$

DOCUMENT: Sediment DIN Remin. (gC/gC/d). This is the specific sed. DIN remin rate based upon an Arrhenius function.

$SDINreminTref = 30$

$SDINremin_E = EXP(SDIN@30_2 * (WatTemp - SDINreminTref))$

DOCUMENT: Sediment DIN Remin. (gC/gC/d). This is the specific sed. DIN remin rate based upon an Arrhenius function.

$WCDIN2c = WCDIN2/VSTvol$

DOCUMENT: Water Column DIN 2 Concentration, VST. (uM). This is the mass (mmoles) over the volume (m³).

$ZSHNupWC = ZSHNupt * VSTwetar * 1000/14$

DOCUMENT: Zostera SH N Uptake. (mmole/d). This is eelgrass Shoot N uptake per unit area per day. From gN/m²/d and the VST area (m²).

VST OTHER PLANKTON

$OP2(t) = OP2(t - dt) + (OP2PNS + OP2_Flx12 - OP2_Flx23 - OP2Exu - OP2_Sed - OP2Resp - OP2Mort) * dt$

INIT OP2 = 373976

DOCUMENT: Other Plankton 2 mass, VST. (gC). INIT = 10 mgChla/m³. Assume 50:1 C:Chl. fraction diatom = 0.67. INIT dia = 0.165 gC/m³. * 1133261 m³ = 373976 gC.

$OP2PNS = OP2_Photo * OP2$

DOCUMENT: Other Plankton 2 Production. (gC/d). From photosynthesis and OP2 biomass.

$OP2_Flx12 = OP_TE12$

DOCUMENT: Other Plankton Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of OP between the NVST & VST habitats.

$OP2_Flx23 = OP_TE23$

DOCUMENT: Other Plankton Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of OP between the VST & NVIT habitats.

$OP2Exu = OPExuk * OP2PNS$

DOCUMENT: Other Plankton 2 Exudation, VST. (gC/d). This is a fraction of OP production.

$OP2_Sed = OPSedk * OP2/hVST$

DOCUMENT: Other Plankton 2 Sedimentation, VST. (gC/d). This is loss to sedimentation from the sed coeff. and the OP mass.

$OP2Resp = OP2 * OP_RT_Ctrl$

DOCUMENT: Other Plankton 2 Respiration, VST. (gC/d). The resp. function * biomass.

$OP2Mort = OP_MortvT * OP2$

DOCUMENT: Other Plankton 2 Mortality, VST. (gC/d). This is loss to mortality from the mort. coeff. and the OP mass.

$OP2c = OP2/VSTvol$

DOCUMENT: Other Plankton Concentration 2, VST. (gC/m3). This is the other plankton concentration in the VST habitat.

$OP2gNm2 = OP2Nremov * 14/1000/VSTwetar$

DOCUMENT: OP 2 N removal gN/m2/d.

$OP2NetCar = OP2NetCvol * hVST$

DOCUMENT: OP 2 Net C by area (gC/m2/d). The volumetric rate * the depth.

$OP2NetCvol = OP2NetP/VSTvol$

DOCUMENT: Other Plankton 2 Net Production, VST. (gC/m3/d). This is volumetric net prod=grosP-resp.

$OP2NetNar = OP2NetCar/Dia_CN_wt$

DOCUMENT: OP 2 Net N demand by area (gC/m2/d). The volumetric rate * the depth.

$OP2NetNvol = OP2NetCvol/Dia_CN_wt$

DOCUMENT: Other Plankton Net N demand by volume. (gN/m3/d).

$OP2NetP = OP2PNS - OP2Resp$

DOCUMENT: Other Plankton 2 Net Production, VST. (gC/d). This is net prod=grosP-resp.

$OP2Nremov = OP_Pmax * OP2_NLim * 1000 * OP2c / 14 / Dia_CN_wt * VSTvol$

DOCUMENT: OP 2 Nitrogen Removal Equation (mmoleN/d).

$NLim * Vmax / C:N * Biomass / 14 * 1000 * VSTvol$ to convert from gN/gN/d to mmoleN/d.

$OP2Nupt = IF(PARo > 0.0) THEN (OP2NetP / Dia_CN_wt * 1000 / 14)$
 $ELSE(0.0)$

DOCUMENT: Other Plankton 2 Nitrogen Uptake, VST. (mmoleN/d). This is the net production converted to N using the Redfield C:N.

$OP2Nuptake2 = IF(PARo > 0.0) THEN (OP2Nremov) ELSE (0.0)$

$OP2_Glim = IF (PARo > 0.0) THEN$

IF (OP2_NLim>OP2_PvI) THEN (OP2_NLim) ELSE (OP2_PvI)
ELSE (0.0)

OP2_NLim = WCDIN2c/(OP_Kdin+WCDIN2c)

DOCUMENT: Other Plankton 3 Nitrogen limitation, NVIT. (unitless). This the hyperbolic tangent curve.

OP2_Photo = OP_Pmax*OP_PT_Ctrl*OP2_Glim

DOCUMENT: Other Plankton 3 Photosynthesis, NVIT. (gC/gC/d). This is the specific diatom photo. function.

OP2_PvI = VSTPAR/(OP_Ik+VSTPAR)

DOCUMENT: Other Plankton 3 Pvs I curve, NVIT. (unitless). The standard hyperbolic tangent curve.

OP_TE12 = IF(FLorEB > 0) THEN (dVol2 * NVSTOPc) ELSE

IF (FLorEB < 0) THEN (dVol2 * OP2c)

ELSE (0.0)

DOCUMENT: Other Plankton Tidal Exchange between Habitats 1 & 2. (gC/d). The physical exchange of OP between the NVST & VST habitats.

OP_TE23 = IF(FLorEB > 0) THEN (dVol3 * OP2c) ELSE

IF(FLorEB < 0) THEN (dVol3 * NVITOPC)

ELSE (0.0)

DOCUMENT: Other Plankton Tidal Exchange between Habitats 2 & 3. (gC/d). The physical exchange of OP between the VST & NVIT habitats.

VST SEDIMENT MICROALGAE

SM2C(t) = SM2C(t - dt) + (SM2Cprod - SM2resp - SM2mort - SM2resus) * dt

INIT SM2C = 4.0

DOCUMENT: Sediment Microalgae Carbon, VST. (gC/m2). The value of 82 mgChla/m2 was converted by multiplying by 50:1 C:Chla and converted to grams to derive 4.0 gC/m2.

SM2Cprod = SM2C*SM2photo

DOCUMENT: Sediment Microalgae Gross C Production, VST. (gC/m2/d).

SM2resp = SM2C*SMRT

DOCUMENT: Sediment Microalgae Respiration, VST. (gC/m2/d). Respiration term for SM.

SM2mort = (SMgrazK*SM2C^2)+(SM2C*SMmCOS)

DOCUMENT: Sediment Microalgae Mortality, VST. (gC/m2/d).

SM2resus = SM2C*SMresusK

DOCUMENT: Sediment Microalgae Resuspension, VST. (gC/m2/d). This is a constant fraction of biomass lost to resuspension (Pinkney, pers. comm.).

BMRsm = 0.05

DOCUMENT: Diatom Respiration Temp Coeff. 2. (/d). Used in exp. curve. 0.01/d given in Cerco&Cole.

KtBsm = 0.069

DOCUMENT: Diatom Respiration Temp Coeff. 1. (/degC). Used in exp. curve.

SM2netC = SM2Cprod-SM2resp

DOCUMENT: Sediment Microalgae Net C Production, VST. (gC/m2/d).

SM2photo = SMPmax*SM2PAR/(SMIk+SM2PAR)

DOCUMENT: Sediment Microalgae Photosynthesis, VST. (gC/gC/d). This is the hyperbolic tangent P vs I for SM.

SMgrazK = 0.045

DOCUMENT: Sediment Microalgal Mortality Coefficient. (m2/gC/d). This is for a quadratic loss term suggested by M. Meyers (from Dominic Ditoro?).

SMIk = 100

DOCUMENT: Sediment Microalgae Ik, VST. (uE/m2/s). 1/2 sat. constant for BM photosynthesis. Calculated from Pinkney&Zingmark 1993. (Pmax=200 umolO2/mgChla/hr. , 0.576/d) to be ca 400. Seems a bit high for our region. Pinkney, pers. comm. also.

SMJDM = 45

SMmCOS = MAX((0-(SMmMax* COS(2*PI*((JD+SMJDM)/365))))).0.0)

SMmMax = 0.05

SMPmax = 0.576

DOCUMENT: Sediment Microalgae Pmax. (gC/gC/d). The value of 200 umoleO2/mgchla/hr (Pinkney & Zingmark 1993) was converted assuming 50:1=C:Chla, C:O=1.0, and 12 hr daylength.

SMresusK = 0.05

DOCUMENT: Sediment Microalgal Resuspension Konstant. (unitless). 5% per day is guess by way of J Pinckney.

SMRT = BMRsm*EXP(KtBsm*(WatTemp-SMRTopt))

DOCUMENT: Sed Micalgae Respiration Temperature Control. (/d). This is the effect of temperature on sm respiration.

SMRTopt = 20

DOCUMENT: Diatom Respiration Optimal Temperature. (degC).

VST ZOSTERA MARINA

ZRRC(t) = ZRRC(t - dt) + (ZCtrans - ZRRlos - ZRRresp - ZRRC2bed) * dt

INIT ZRRC = 25

DOCUMENT: Initial RR concentration (gC/m2) taken from Buzzelli '93: Moore et al., SAV Habitat Survey; both at Goodwin Isl. S:RR biomass=1.0 in winter.

ZCtrans = IF(ZSHCFB < 1.0) THEN (ZCpot*ZSHCnet)

ELSE(ZSHCnet)

DOCUMENT: Zostera Shoot-RR translocation. (gC/m2/d).

{ old, one-way, WW-limtd flow:

$ZC_{pot} * ZSHC * \text{MAX}(ZSHCP_{\text{prod}} - ZSHR_{\text{resp}}, 0.0) * (1 - ZosRRFB)$

new, potentially 2-way, unlimited flow:
 $ZC_{pot} * ZSHC * (ZSHCP_{\text{prod}} - ZSHR_{\text{resp}})$

another new, 2-way function with shoot biomass feedback
 $ZSHFB * ZSHC * (ZSHCP_{\text{prod}} - ZSHR_{\text{resp}})$

$ZRR_{\text{los}} = ZRRC * (ZSH_{\text{los}} / ZSHC)$

DOCUMENT: Root-rhizome mortality. (gC/ m²/d). This is biomass loss of RR proportional to the fractional loss of Shoot biomass.

$ZRR_{\text{resp}} = ZRRC * ZRR_r$

DOCUMENT: Zostera RR respiration. (gC/m²/d).

$ZRRC2_{\text{bed}} = \text{if } ZosRRFB = 1.0 \text{ then } \text{max}(ZC_{\text{trans}}, 0.0) \text{ else } 0.05 * \text{max}(ZC_{\text{trans}}, 0.0)$

DOCUMENT: Zostera RR carbon to Bed Storage. (gC/m²/d).

When ZRRC reaches max (=ZRRBiomax) and there is available C to be xloc'd downward, this excess carbon is shunted to a proxy for bed expansion or long-term storage. NOTE: if flow is unidir., this carbon becomes unavail for later use, should plant receive insufficient light for net production. 0.05 is attempt to push 5% of translocated net prod into the bed store when RRC is not at max.

$ZRRC_BedStor(t) = ZRRC_BedStor(t - dt) + (ZRRC2_{\text{bed}}) * dt$

INIT ZRRC_BedStor = 0

DOCUMENT: This is a proxy for below-ground expansion. gC/m²

$ZRRC2_{\text{bed}} = \text{if } ZosRRFB = 1.0 \text{ then } \text{max}(ZC_{\text{trans}}, 0.0) \text{ else } 0.05 * \text{max}(ZC_{\text{trans}}, 0.0)$

DOCUMENT: Zostera RR carbon to Bed Storage. (gC/m²/d).

When ZRRC reaches max (=ZRRBiomax) and there is available C to be xloc'd downward, this excess carbon is shunted to a proxy for bed expansion or long-term storage. NOTE: if flow is unidir., this carbon becomes unavail for later use, should plant receive insufficient light for net production. 0.05 is attempt to push 5% of translocated net prod into the bed store when RRC is not at max.

$ZRRN(t) = ZRRN(t - dt) + (ZRRN_{\text{upt}} - ZN_{\text{trans}} - ZRRN_{\text{los}} - ZRRN_{\text{stor}}) * dt$

INIT ZRRN = 1.25

DOCUMENT: Zostera RR N storage (gN/m²). The initial value is set at the minimum

$ZRRN_{\text{upt}} = ZRRN * ZRRN_{\text{mm}}$

DOCUMENT: Zostera RR N Uptake. (gN/m²/d). This is eelgrass RR N uptake per unit area per day.

$ZN_{\text{trans}} = (ZSHN_{\text{demand}} - ZSHN_{\text{upt}}) * (1 - ZRRCN_{\text{fb}}) * (ZSHCN_{\text{fb}})$

{ IF(ZSHC:N > ZSHCNopt) THEN((ZSHNdemand-ZSHNupt)*(ZRRNFB)*(1-ZSHNFB)) ELSE(0.0) }

DOCUMENT: Zostera upwards N translocation. The difference between Zostera shoot N demand and the shoot uptake. The units are in gN/m²/hr. Mitigated by N status of RR tissue. {OLD: Set at 35% of uptake rate. }

$ZRRN_{\text{los}} = 0.90 * ZRR_{\text{los}} / ZRRC * ZRRN$

DOCUMENT: Zostera RootRhizome Nitrogen Loss. (gN/m²/d). This is particulate loss of zostera RR nitrogen via mortality at a fraction consistent with RR C loss.

$$\text{ZRRNstor} = 0.0 * (\text{ZRRc2bed} / \text{ZRRmaxCN})$$

DOCUMENT: Zostera RR N to storage. (gN/m²/d). This shunts RR nitrogen to the bed store based on the RR C shunted and the maximum RR C:N.

{ When ZRRc reaches max (=ZRRBiomax) and there is available C to be xloc'd downward, this excess carbon is shunted to a proxy for bed expansion or long-term storage. NOTE: if flow is unidir., this carbon becomes unavail for later use, should plant receive insufficient light for net production. 0.05 is attempt to push 5% of translocated net prod into the bed store when RRC is not at max. }

$$\text{ZRRN_BedStor}(t) = \text{ZRRN_BedStor}(t - dt) + (\text{ZRRNstor}) * dt$$

$$\text{INIT ZRRN_BedStor} = 0$$

DOCUMENT: This is the nitrogen component for below-ground expansion. gN/m²

$$\text{ZRRNstor} = 0.0 * (\text{ZRRc2bed} / \text{ZRRmaxCN})$$

DOCUMENT: Zostera RR N to storage. (gN/m²/d). This shunts RR nitrogen to the bed store based on the RR C shunted and the maximum RR C:N.

{ When ZRRc reaches max (=ZRRBiomax) and there is available C to be xloc'd downward, this excess carbon is shunted to a proxy for bed expansion or long-term storage. NOTE: if flow is unidir., this carbon becomes unavail for later use, should plant receive insufficient light for net production. 0.05 is attempt to push 5% of translocated net prod into the bed store when RRC is not at max. }

$$\text{ZRRPOC}(t) = \text{ZRRPOC}(t - dt) + (\text{ZRRlos} + \text{ZSHPOCsed}) * dt$$

$$\text{INIT ZRRPOC} = 0$$

$$\text{ZRRlos} = \text{ZRRc} * (\text{ZSHlos} / \text{ZSHc})$$

DOCUMENT: Root-rhizome mortality. (gC/ m²/d). This is biomass loss of RR proportional to the fractional loss of Shoot biomass.

$$\text{ZSHPOCsed} = \text{ZfPOCdep} * \text{ZSHlos}$$

DOCUMENT: Zostera Shoot POC Production. (gC/m²/d). This is simply the shoot loss rate * the fraction deposited.

$$\text{ZRRPON}(t) = \text{ZRRPON}(t - dt) + (\text{ZRRNlos}) * dt$$

$$\text{INIT ZRRPON} = 0$$

DOCUMENT: Zostera RR PON. This is RR PON loss through mortality. gN/gC

$$\text{ZRRNlos} = 0.90 * \text{ZRRlos} / \text{ZRRc} * \text{ZRRN}$$

DOCUMENT: Zostera RootRhizome Nitrogen Loss. (gN/m²/d). This is particulate loss of zostera RR nitrogen via mortality at a fraction consistent with RR C loss.

$$\text{ZSHc}(t) = \text{ZSHc}(t - dt) + (\text{ZSHcProd} - \text{ZSHResp} - \text{ZCtrans} - \text{ZSHlos}) * dt$$

$$\text{INIT ZSHc} = 25$$

DOCUMENT: Zostera Shoot Carbon (gC/m²). Taken from Buzzelli '93; Moore et al., SAV Habitat Survey; both at Goodwin Isl. Initialized for January.

$$\text{ZSHcProd} = \text{ZSHPhoto} * \text{ZSHc}$$

DOCUMENT: Zostera Shoot C Gross Production. (gC/m²/d). This is gross shoot production.

{ The MIN function accomodates production rates based upon other factors (e.g. nutrients, temperature). }

$$\text{ZSHResp} = \text{ZSHR} * \text{ZSHc}$$

DOCUMENT: Zostera Shoot Respiration. (gC/m²/d) Based upon Wetzel and Neckles (1986) derivation.

ZCtrans = IF(ZSHCFB < 1.0) THEN (ZCpot*ZSHCnet)
ELSE(ZSHCnet)

DOCUMENT: Zostera Shoot-RR translocation. (gC/m²/d).

{ old, one-way, WW-limtd flow:

ZCpot*ZSHC*MAX(ZSHCProd-ZSHResp,0.0)*(1-ZosRRFB) new, potentially 2-way, unlimited flow:

ZCpot*ZSHC*(ZSHCProd-ZSHResp) another new, 2-way function with shoot biomass feedback

ZSHFB*ZSHC*(ZSHCProd-ZSHResp)}

ZSHlos = ZSHTotm*ZSHC

DOCUMENT: Zostera Shoot Mortality. (gC/m²/d). This is the sum of the WetNeck shoot mortality and fall shoot senescence functions multiplied by the shoot carbon biomass.

ZSHN(t) = ZSHN(t - dt) + (ZNtrans + ZSHNupt - ZSHNlos) * dt

INIT ZSHN = 1.8

DOCUMENT: Zostera Shoot N Storage (gN/m²). The initial value is set at the minimum.

ZNtrans = (ZSHNdemand-ZSHNupt)*(1-ZRRCNfb)*(ZSHCNfb)

{ IF(ZSHC:N > ZSHCNopt) THEN((ZSHNdemand-ZSHNupt)*(ZRRNFB)*(1-ZSHNFB)) ELSE(0.0) }

DOCUMENT: Zostera upwards N translocation. The difference between Zostera shoot N demand and the shoot uptake. The units are in gN/m²/hr. Mitigated by N status of RR tissue.

{ OLD: Set at 35% of uptake rate. }

ZSHNupt = ZSHN*ZSHNmm

DOCUMENT: Zostera Shoot Nitrogen Uptake. (gN/m²/d). This is the shoot nitrogen uptake per unit area per day.

ZSHNlos = ZSHlos/ZSHC*ZSHN

DOCUMENT: Zostera Shoot Nitrogen Loss. (gN/m²/d). This is particulate loss of zostera shoot nitrogen via mortality at a fraction consistent with shoot carbon loss.

ZSHPOC(t) = ZSHPOC(t - dt) + (ZSHlos) * dt

INIT ZSHPOC = 0

DOCUMENT: Zostera shoot POC. This is the cumulative shoot mortality term. In gC unless space introduced.

ZSHlos = ZSHTotm*ZSHC

DOCUMENT: Zostera Shoot Mortality. (gC/m²/d). This is the sum of the WetNeck shoot mortality and fall shoot senescence functions multiplied by the shoot carbon biomass.

ZSHPON(t) = ZSHPON(t - dt) + (ZSHNlos) * dt

INIT ZSHPON = 0

DOCUMENT: Zostera Shoot PON. This is shoot PON loss through mortality. gN/gC

ZSHNlos = ZSHlos/ZSHC*ZSHN

DOCUMENT: Zostera Shoot Nitrogen Loss. (gN/m²/d). This is particulate loss of zostera shoot nitrogen via mortality at a fraction consistent with shoot carbon loss.

BMRzm = 0.045

DOCUMENT: Zostera Respiration Factor. (/d). From WES Ches. Bay model. 0.01/d or 0.003/d (Jan-May in salt water only).

KtBzm = 0.069

DOCUMENT: Zostera Respiration Temp Coeff. 1. (/degC). Used in exp. curve. From WES Ches. Bay model.

ZAlpha = 0.015

DOCUMENT: This is the initial slope of the PvsI curve, data taken from Wetzel and Penhale 1983. This value is a unit conversion of the mean value reported. Units are m²/uE (hrs to days conversion was necessary)

ZCpot = 0.25

DOCUMENT: This represents a maximum of 25% of Shoot Production that can be basipetally translocated. Dependent upon Shoot Net Prod and potentially RR respiration. Introduced as converter in order to eventually fluctuate the value given other factors.

ZfPOCdep = 0.50

DOCUMENT: Zostera marina Fraction POC deposited. (unitless). 50% of the Zostera Shoot POC stays in the NVST habitat. 50% transported. These values are mere guesses.

ZIk = 57.5

DOCUMENT: Zostera marina Ik. (uE/m²/s). The saturating light intensity for Zostera photosynthesis. Mean value from Evans et al. 1986.

ZIk_b = (1268*ZPmaxT-2.66)

DOCUMENT: Zostera Ik w/ Temp. (uE/m²/s). This is the Wetzel & Neckles function for Zostera Shoot Ik when Pmax is /d.

ZmJDm = 333

DOCUMENT: Zostera marina Julian Day Mort. This is the day in the fall Zost shoot mortality begins.

ZmPT1 = 0.004

DOCUMENT: Diatom Photosynthesis Temp Coeff. 1. (/degC²). Used in exp. curve.

ZmPT2 = 0.006

DOCUMENT: Diatom Photosynthesis Temp Coeff. 2. (/degC²). Used in exp. curve.

ZmPTmax = 0.01

ZmRTopt = 20

DOCUMENT: Zostera Respiration Optimal Temperature. (degC).

ZmSHFMk = 0.0135

DOCUMENT: Zostera marina Shoot Fall Mort. K. (/d).

ZmSHFmort = ZmSHFMk*(IF (MOD(JD.365)<=ZmJDm) THEN (EXP(-ZmSHm1*(MOD(JD.365)-ZmJDm)²)) ELSE (EXP(-ZmSHm2*(ZmJDm-MOD(JD.365))²)))

DOCUMENT: Zostera Shoot fall Mort. (gC/gC/d). This is the maximum mortality rate function for fall shoot loss of Zostera. (was 0.02075, too high)

ZmSHm1 = 0.0003

DOCUMENT: Zostera Shoot Mort 1. This is a constant in the Zostera shoot loss equation.

ZmSHm2 = 0.0005

DOCUMENT: Zostera Shoot Mort 2. This is a constant in the Zostera shoot loss equation.

Zm_PTopt = 20

DOCUMENT: Diatom Photosynthesis Optimal Temperature. (degC). Like most everything else, estimated @ 20. Reduced to 15 to better represent the spring freshet.

Zm_PT_Ctrl = ZmPTmax*(IF (WatTemp<=Zm_PTopt) THEN
(EXP(-ZmPT1*(WatTemp-Zm_PTopt)^2)) ELSE
(EXP(-ZmPT2*(Zm_PTopt-WatTemp)^2)))

DOCUMENT: Zostera Photosynthesis Temperature Control. (/d). This is the effect of temperature on Zostera photosynthesis.

ZNtotupt = ZRRNupt+ZSHNupt

DOCUMENT: Zostera total Nitrogen Uptake. (gN/m2/d). This is the sum of shoot and RR uptake.

ZosRRFB = MIN(MAX(ZRRC-ZRRlim,0)/(ZRRbiomax-ZRRlim),1.0)

DOCUMENT: Zostera RR Feedback. (unitless). This is the Wiegert-Wetzel feedback function for basipetal translocation and RR production.

ZPmax = 0.007

DOCUMENT: Zostera Leaf Pmax. From Wetzel and Penhale, 1983. Mar. Tech. Soc. J., 17(2):22-31. From P vs I curves using clean plant leaves and the C14. based upon 40% of leaf biomass is carbon. gC/gshootC/hr.

ZPmaxT = 1.2 * (0.0025*WatTemp+0.0049)*(1-MAX(WatTemp-25.0)/10)

{0.002} DOCUMENT: Zostera Pmax with Temp. (gC/gC/d). Biphasic relationship with water temperature: optimum at 25C, declines to zero at 35C. From Wetzel and Neckles, '86.
{0.000162??}

ZRRbiomax = 200

DOCUMENT: Maximum supportable RR biomass (g/m2) taken from Wetzel and Neckles 1986.

ZRRCN = ZRRC/ZRRN

ZRRCNfb = MIN(MAX(ZRRCN-ZRRCNmin,0)/(ZRRCNmax-ZRRCNmin),1.0)

ZRRCNmax = 28

DOCUMENT: Zostera RR C:N maximum. (unitless weight ratio). Determined for April in Buzzelli thesis.

ZRRCNmin = 15

DOCUMENT: Zostera RR C:N minimum. (unitless weight ratio). Determined for March in Buzzelli thesis.

ZRRCNopt = 25

DOCUMENT: Optimal Zostera RR C:N ratio. From Buzzelli 1991 thesis.

ZRRKsN = 30

DOCUMENT: Zostera RR Ks Nitrogen. 30uM NH4 concentration is value provided in Iizumi & Hattori

1981

$ZRRlim = 100$

DOCUMENT: RR biomass concentration (gC/m²) above which density dependent factors could be in effect.

$ZRRmaxCN = 30$

DOCUMENT: Zostera RR maximum C:N. Given as 30 gC/gN (approximated from Buzzelli thesis).

$ZRRNdemand = ZRRnetC/ZRRCN$

DOCUMENT: Zostera RR nitrogen demand. (gC/m²/d). The net C production / the actual RR C:N ratio.

$ZRRNmm = ZSHCRelGro * ZRRVmN * (VSTsDIN / (ZRRKsN + VSTsDIN)) * (ZRRCNfb)$

DOCUMENT: Zostera RR N Uptake Specific Rate. (gN/gN/d). This is a Michaelis-Menten function for eelgrass RR N uptake from sediment DIN. Process is adjusted for the relative photosynthetic rate (i.e., there is no net upt in dark) using the Relative Growth term.

$ZRRr = ZRRr@20 * ZRRrQ10^{(WatTemp-20)}$

DOCUMENT: Spartina alterniflora RR Respiration. (gC/gC/d). This is the specific Sa RR resp. Arrhenius function.

$ZRRr@20 = 0.0005$

DOCUMENT: Spartina alterniflora RR Respiration at 20degC. (gC/gC/d). This is the RR resp. rate at the optimum temperature for use in an Arrhenius function.

$ZRRrQ10 = 1.25$

DOCUMENT: Spartina alterniflora RR Q10 value. This is the Q10 for use in the calculation of RR respiration.

$ZRRVmN = 0.072$

DOCUMENT: Zostera RootRhizome Vmax Nitrogen. (gN/gN/d). Average rate measured in Buzzelli 1991 thesis was 0.006 gN/gN/hr * 12 hours gives 0.072.

$ZRT_Ctrl = BMRzm * EXP(KtBzm * (WatTemp - ZmRTopt))$

DOCUMENT: Diatom Respiration Temperature Control. (/d). This is the effect of temperature on diatom respiration.

$ZSHbiomax = 200$

$ZSHCDW = 0.4$

DOCUMENT: Zostera Shoot Carbon. A value of 0.4 gC/gdw shoot has been chosen as a converter for other parameters on a gdw basis.

$ZSHCFB = MIN(MAX(ZSHC - ZSHlim, 0) / (ZSHbiomax - ZSHlim), 1.0)$

DOCUMENT: This is the Wiegert-Wetzel feedback function for basipetal translocation and RR production.

$ZSHCN = ZSHC / ZSHN$

$ZSHCnet = ZSHCProd - ZSHResp$

DOCUMENT: Zostera Shoot Net Carbon Production. (gC/m²/d). This is difference between gross P and respiration.

$ZSHCNfb = \text{MIN}(\text{MAX}(ZSHCN - ZSHCNmin, 0) / ((ZSHCNmax - ZSHCNmin)), 1.0)$

$ZSHCNmax = 22$

DOCUMENT: Zostera Shoot C:N maximum. (unitless weight ratio). Determined for June in Buzzelli thesis.

$ZSHCNmin = 12$

DOCUMENT: Zostera Shoot C:N minimum. (unitless weight ratio). Determined for February in Buzzelli thesis.

$ZSHCNopt = 16$

$ZSHCRelGro = ZSHPhoto / ZPmaxT$

DOCUMENT: Zostera Shoot Relative Growth. (unitless ratio, 0..1). This can be used to scale processes to photosyn (C fixation) rate; e.g., nutrient uptake. unitless.

$ZSHKsN = 10$

DOCUMENT: Zostera Shoot Ks Nitrogen. This value of 10 μM N was estimated from Short & McRoy 1984, Zimmerman et al. 1987 (by way of Thursby and Harlin 1981), and Iizumi and Hattori 1982. Short&McRoy data were iteratively fit to an MM expression to estimate Ks and Vmax.

$ZSHlim = 100$

$ZSHmort = (0.0175 - 0.0125 * \cos(2 * \pi * JD / 365)) * \text{MAX}(\text{WatTemp} - 20.0) / (30 - 20)$

{OLD: $\text{MAX}(\text{WatTemp} - 10.0) / (30 - 10)$ }

DOCUMENT: Zostera Shoot Mortality. (gC/gC/d). Zostera shoot carbon loss through mortality.

$ZSHNCrate = ZSHNup / ZSHN * ZSHC$

DOCUMENT: Zostera Shoot Nitrogen-to-Carbon rate. ($\text{gC/m}^2/\text{hr}$). This is a productivity rate based upon total plant nitrogen uptake ($\text{gN/m}^2/\text{hr}$).

$ZSHNdemand = (ZSHCProd - ZSHResp) / (ZSHCNopt)$

DOCUMENT: Zostera Shoot Nitrogen Demand. ($\text{gN/m}^2/\text{d}$). The shoot net C production rate in nitrogen units.

$ZSHNmm = (ZSHCNfb) * ZSHCRelGro * ZSHVmN * (\text{WCDIN}2c / (ZSHKsN + \text{WCDIN}2c))$

DOCUMENT: Eelgrass Shoot N Uptake Specific Rate. (gN/gN/d). This is a Michaelis-Menten function for DIN uptake by eelgrass leaves. Process can be adjusted for the relative photosynthetic rate (i.e., there is no nut upt in dark), but this causes a circular connection given that N+P influence C production.

$ZSHPhoto = ZPmaxT * \text{PARZleaf} / (ZIk + \text{PARZleaf})$

DOCUMENT: Zostera Shoot Photosynthesis. (gC/gC shoot/d). Hyperbolic tangent function, P vs I.

$ZSHR = 1.5 * (ZSHPhoto * (0.00317 * \text{WatTemp} + 0.105) + \text{EXP}(0.137 * \text{WatTemp} - 10.1))$

DOCUMENT: Zostera Shoot Respiration. (gC/gC/d). This is the specific respiration function for zostera shoots.

$ZSHTotm = ZmSHFmort + ZSHmort$

$ZSHVmN = 0.021$

DOCUMENT: Zostera Shoot Vmax Nitrogen. (gN/gN/d). The value of 3.18 $\mu\text{moleN/gdw/hr}$ from Short&McRoy (1984) was converted to these units using 12 hrs/day and 0.0257 gN/gdwShoots (from CBuzz Thesis) to derive 0.021/d. {The value of 0.01 gN/gNshoot/hr was taken from Short & McRoy 1984, Iizumi & Hattori 1982, and Pederson & Borum 1993 and converted to days using 12 hours.

Short&McRoy data were iteratively fit to an MM expression to estimate Ks and Vmax. }
{ It was then corrected to gN/gC shoot/hr using a molar C:N=20. }

ZOSTERA EPIPHYTON

$ZepiC(t) = ZepiC(t - dt) + (ZEpiProd - ZEpiResp - ZEpiGraz - ZEpiLoss) * dt$

INIT ZepiC = 5

DOCUMENT: Zostera epiphyton Carbon. (gC/m2). The initial value of 5 was estimated from the KMoore GI intensive data.

$ZEpiProd = ZEpi_Photo * ZepiC$

DOCUMENT: Zostera Epiphyte C Production. (gC/m2/d). From WetNeck, the photosynthesis*biomass*(1-total FB). F0205

$ZEpiResp = ZEpiRT_Ctrl * ZepiC$

$ZEpiGraz = ZEpiGrazk * ZepiC^2$

DOCUMENT: Grazing Rate on Zos Epiphytes (g C/m2/day). From WetNeck model.
 $0.805 * (MAX((WatTemp - 1.0), 0.0) / (30 - 10))$

$ZEpiLoss = (ZEpi_to_Det + ZEpimontk) * ZepiC$

DOCUMENT: Zostera Epiphyte Biomass Loss (gC/m2/d). A combination of a constant fractional biomass loss and a mortality function based on the ratio between Epi and Zostera Shoot biomass.

BMRepi = 0.045

DOCUMENT: Epiphyte Respiration Factor. (/d). From WES Ches. Bay model. 0.01/d or 0.003/d (Jan-May in salt water only).

CO2 = 25

DOCUMENT: CO2 concentration in the water. (gC/m3). From WetNeck for use in productivity FB functions. X02

EpiPmax = 0.01

KtBepi = 0.069

DOCUMENT: Epiphyte Respiration Temp Coeff. 1. (/degC). Used in exp. curve. From WES Ches. Bay model.

$ZEpiCO2D = 1 / ((ZEpiCO2max - ZEpiCO2lim) + 0.1E-15)$

DOCUMENT: Zostera Epiphyte CO2 max/lim. (unitless). A combination of the maximum and limitation terms for use in FB equations. D0205

$ZEpiCO2FB = MAX((1 - (MAX((CO2 - ZEpiCO2lim), 0.0) * ZEpiCO2D)), 0.0)$

DOCUMENT: Zostera Epiphyte CO2 Feedback. (unitless). From WetNeck model. This is the donor controlled FB term for ZEpi production. FB0205

$ZEpiCO2FBp = MAX((1 - ZEpiCO2FB), 0.0)$

DOCUMENT: Zostera Epiphyte CO2 Feedback. (unitless). From WetNeck model. This is 1.0 minus the donor controlled FB term for ZEpi production. FBP0205

ZEpiCO2lim = 5

DOCUMENT: Zostera Epiphyte CO2 limitation term. (gC/m2). This is the limitation value for the

donor controlled FB for Epiphyte production. G0205

$Z_{EpiCO2max} = 15$

DOCUMENT: Zostera Epiphyte CO₂ maximum term. (gC/m²). This is the maximum value for the donor controlled FB for Epiphyte production. A0205

$Z_{EpiD} = 1/((Z_{Epilim}-Z_{Epimax})+0.1E-15)$

DOCUMENT: Zostera Epiphyte max/lim. (unitless). A combination of the maximum and limitation terms for use in FB equations. D0505

$Z_{EpiFB} = 1.0-(MAX((1-(MAX((Z_{EpiLeaf_Ratio}-Z_{Epimax}),0.0)*Z_{EpiD})),0.0))$

DOCUMENT: Zostera Epiphyte Self Regulating Feedback. (unitless). From WetNeck model. This is the recipient controlled FB term for Z_{Epi} production. FB0505

$Z_{EpiGrazk} = 0.001$

$Z_{EpiLeaf_Ratio} = IF(Z_{SHC} > 0.0) THEN(Z_{epiC}/Z_{SHC}) ELSE (0.0)$

DOCUMENT: Zostera Epi:Leaf Biomass Ratio. (unitless weight ratio). Used in PAR attenuation due to epiphytes.

$Z_{Epilim} = 2.0$

DOCUMENT: Zostera Epiphyte limitation term. (gC/m²). This is the limitation value for the self controlled FB for Epiphyte production. G0505

$Z_{Epimax} = 1.0$

DOCUMENT: Zostera Epiphyte max term. (gC/m²). This is the max value for the self controlled FB for Epiphyte production. A0505

$Z_{EpiMet} = MAX((1-(Z_{Epi_R}/(Z_{Epi_Photo}+0.1E-15))),0.0)$

DOCUMENT: Zostera Epiphyte Metabolic Correction. (unitless??). From WetNeck, partly a ratio between Z_{Epi} respiration and Z_{Epi} photosynthesis. C0205

$Z_{Epimortk} = 0.0002083*0.0$

DOCUMENT: Zostera Epiphyte mortality coef. (gC/gC/day). From WetNeck = 0.0002083 per day. This is a fraction of a percent per day of epiphyte biomass that is lost.

$Z_{epiRTopt} = 20$

DOCUMENT: Epiphyte Respiration Optimal Temperature. (degC).

$Z_{EpiRT_Ctrl} = BM_{Repi}*EXP(Kt_{Bepi}*(WatTemp-Z_{epiRTopt}))$

DOCUMENT: Diatom Respiration Temperature Control. (/d). This is the effect of temperature on diatom respiration.

$Z_{EpiTFB} = MAX((1.0-(Z_{EpiCO2FBp}*(1.0-(Z_{EpiFB}*Z_{EpiMet})))),0.0)$

DOCUMENT: Zostera Epiphyte Total Feedback. (unitless). From WetNeck model. This is the recipient + donor controlled FB term for Z_{Epi} production. TF0205

$Z_{epi_Glim} = IF (PAR_o > 0.0) THEN$

$IF (Z_{epi_Nlim}>Z_{epi_PvI}) THEN (Z_{epi_Nlim}) ELSE (Z_{epi_PvI})$

$ELSE (0.0)$

$Z_{epi_Ik} = 50 + (100*(MAX((WatTemp-10),0.0)/(30-10)))$

DOCUMENT: Zostera Epiphyte Ik. (uE/m²/s ??). Taken from the WetNeck Grazer model.

$Z_{epi_Nlim} = WCDIN2c / (OP_Kdin + WCDIN2c)$

DOCUMENT: Other Plankton 3 Nitrogen limitation, NVIT. (unitless). This the hyperbolic tangent curve.

$Z_{epi_Photo} = Z_{epi_Glim} * Z_{epi_Pmax}$

DOCUMENT: Zostera Epiphyte Photosynthesis. (gC/gC/d). Growth limitation chooses between N and I effects.

$Z_{epi_Pmax} = (0.0091 * WatTemp * (1.0 - (MAX((WatTemp - 25), 0.0) / (45 - 25))))$

DOCUMENT: Zostera Epiphyte Pmax (gC/gC/d). Taken from the WetNeck Grazer model. PM05 (Grazer model appears to be in HOURS, I multiplied $0.0003801 * 12$ hours = 0.00456 to derive DAYS).

$Z_{epi_PvI} = VSTPAR / (Z_{epi_Ik} + VSTPAR)$

DOCUMENT: Other Plankton 3 Pvs I curve, NVIT. (unitless). The standard hyperbolic tangent curve.

$Z_{epi_R} = (0.5 * (0.5 * ((0.0104 * WatTemp) + 0.3432) * Z_{epi_Photo}) + \exp((0.1370 * WatTemp) - 10.09))$

DOCUMENT: Zostera Epiphyte Respiration. (gC/gC/d). From WetNeck model. R0502.

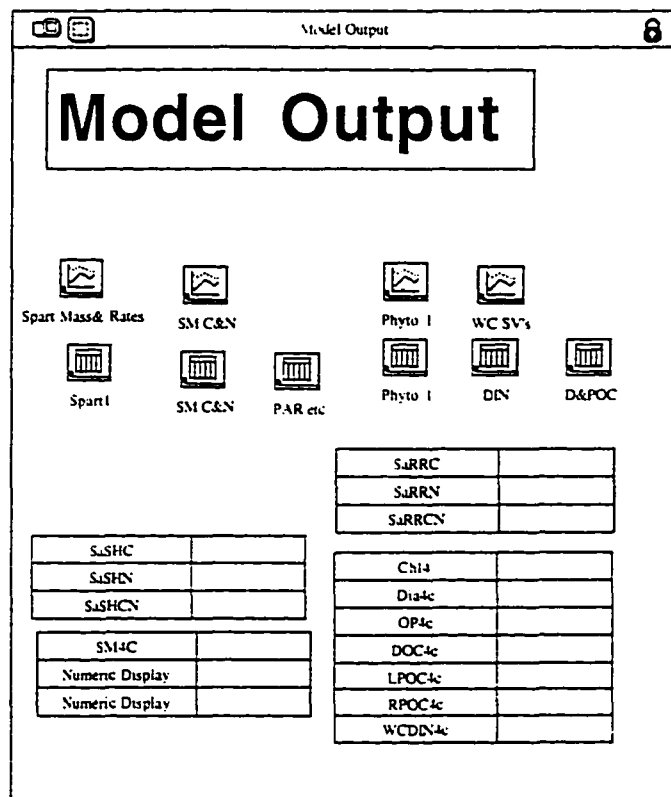
$Z_{epi_to_Det} = (Z_{epi_Leaf_Ratio} * Z_{SHTotm})$

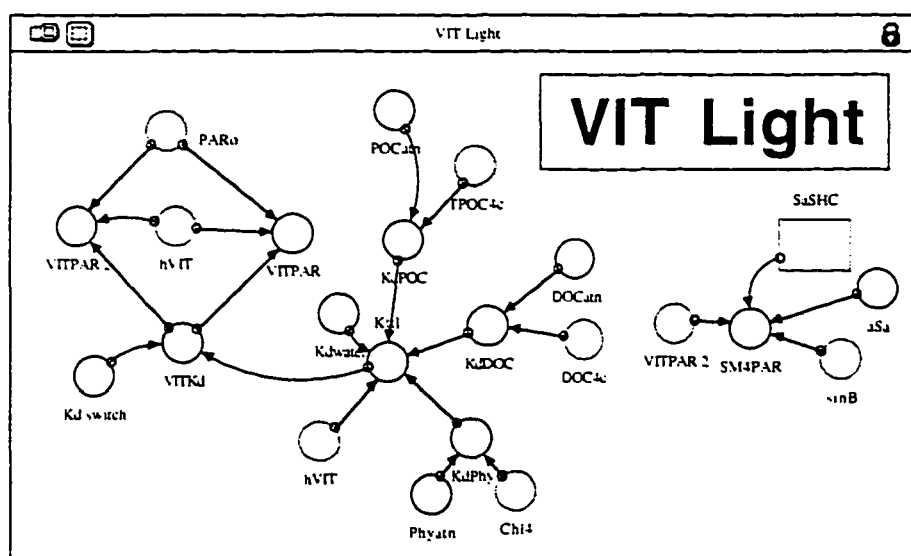
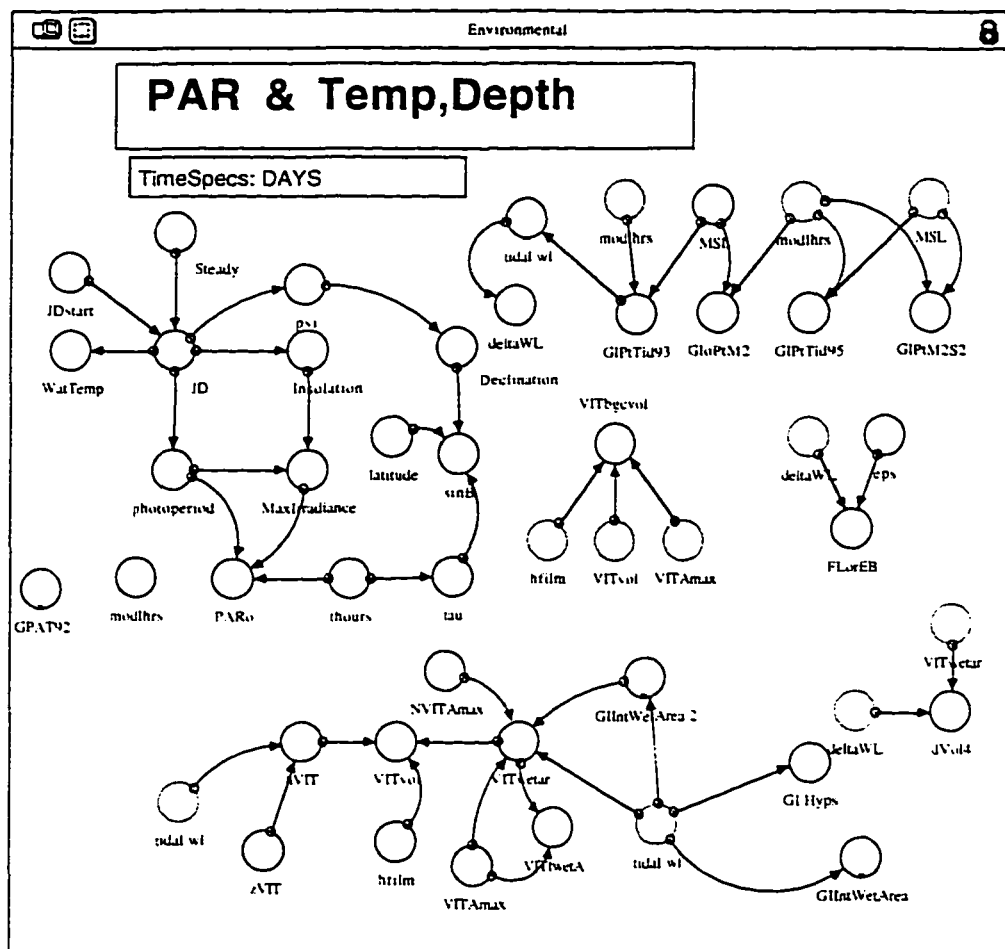
DOCUMENT: Zostera Epiphyte loss to detritus. (gC/gC/d). From WetNeck Grazer model. Simply specific Zostera leaf loss rate * Epi:Leaf ratio.

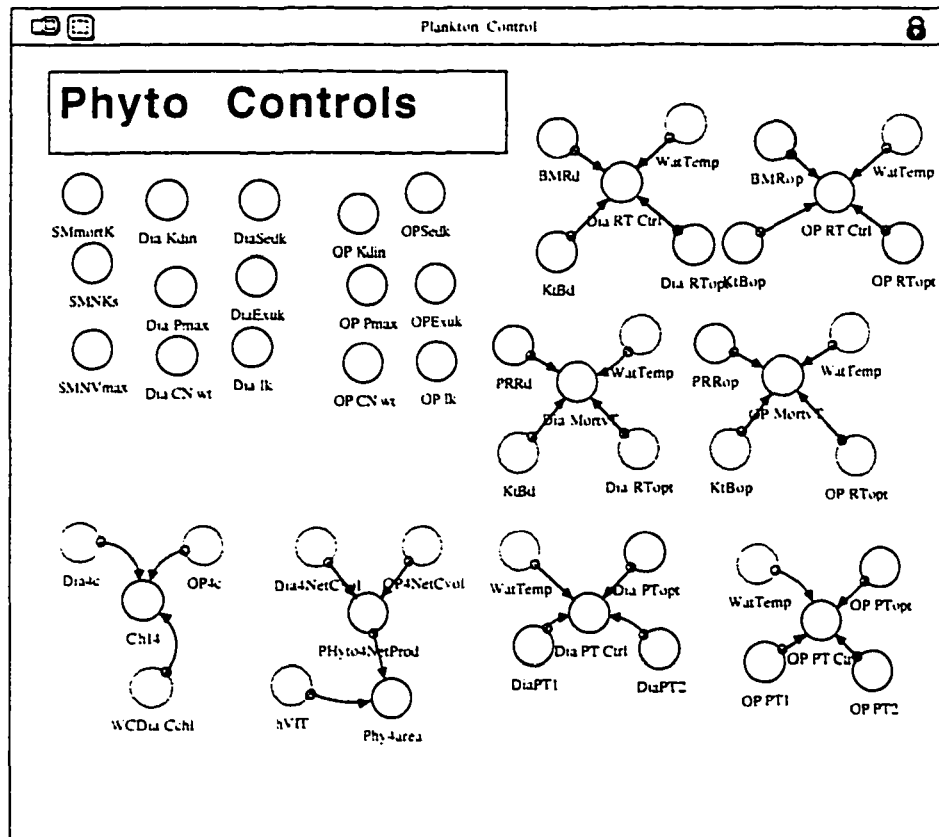
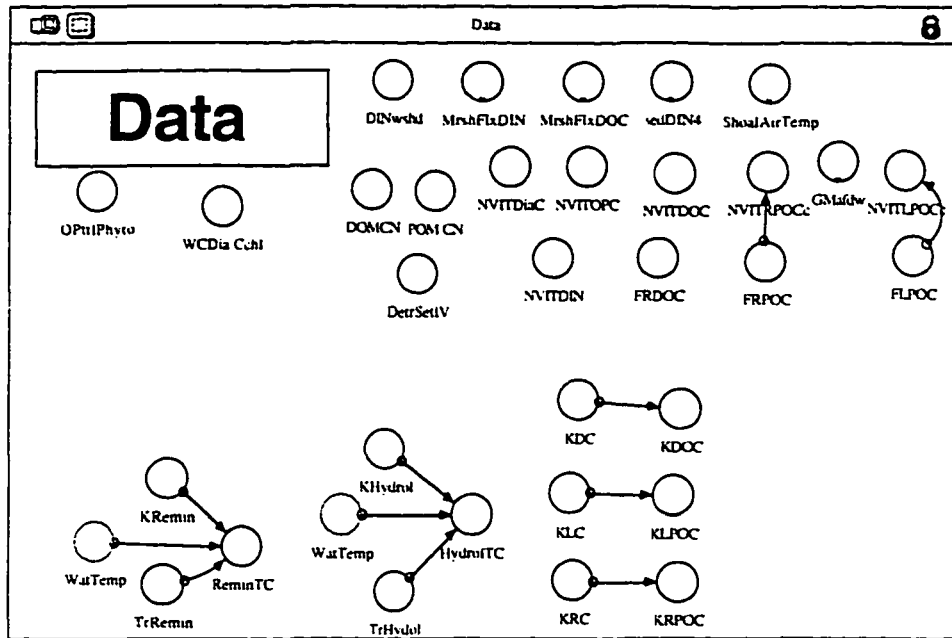
$Z_{epi_Grazers} = GRAPH(TIME)$

(0.00, 0.00), (33.2, 0.00), (66.4, 0.015), (99.5, 0.045), (133, 0.105), (166, 0.28), (199, 0.415), (232, 0.47), (265, 0.395), (299, 0.23), (332, 0.1), (365, 0.02)

Goodwin Islands Vegetated Intertidal Habitat Model Adapted from the Goodwin Islands Ecosystem Linked Littoral Zone Spatial Model C.P. Buzzelli and M.B. Meyers. Spartina model beg. 4 Oct 95

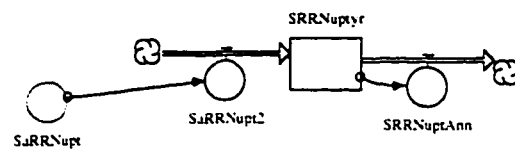
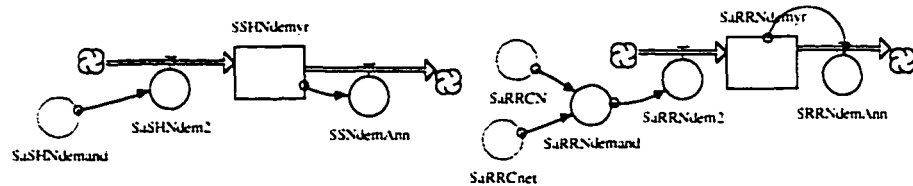
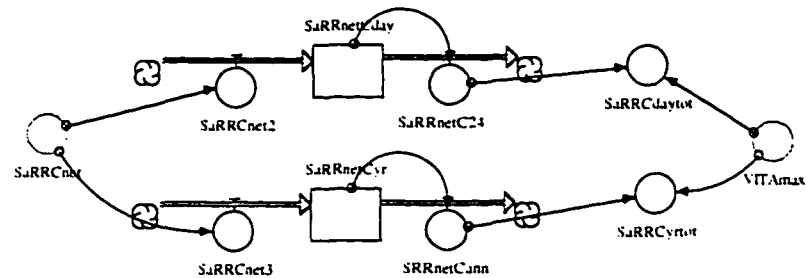
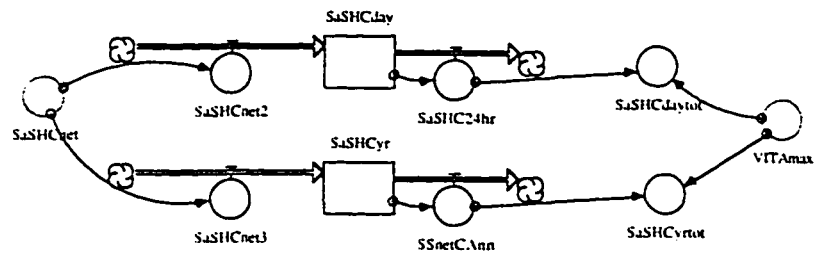


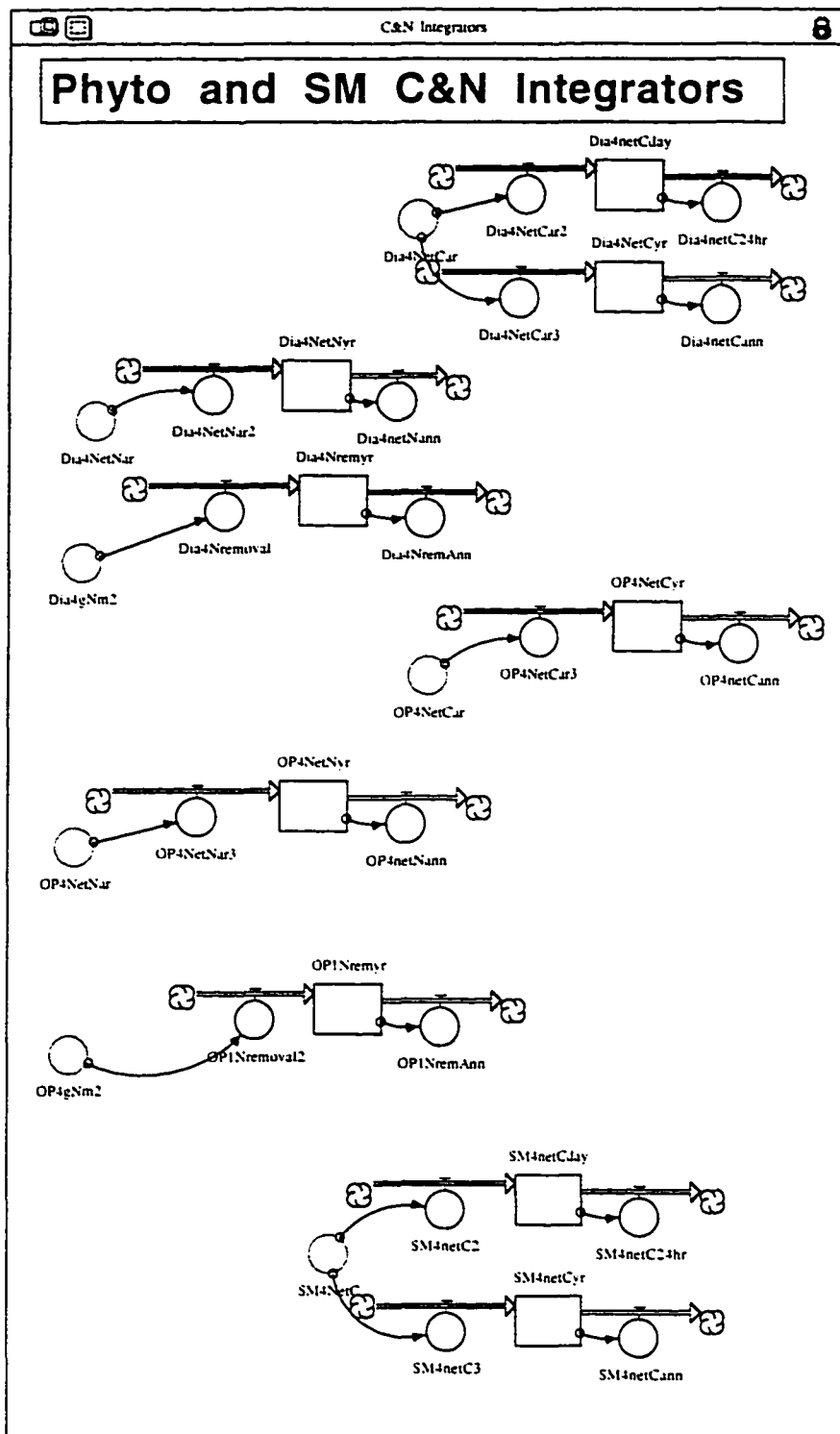


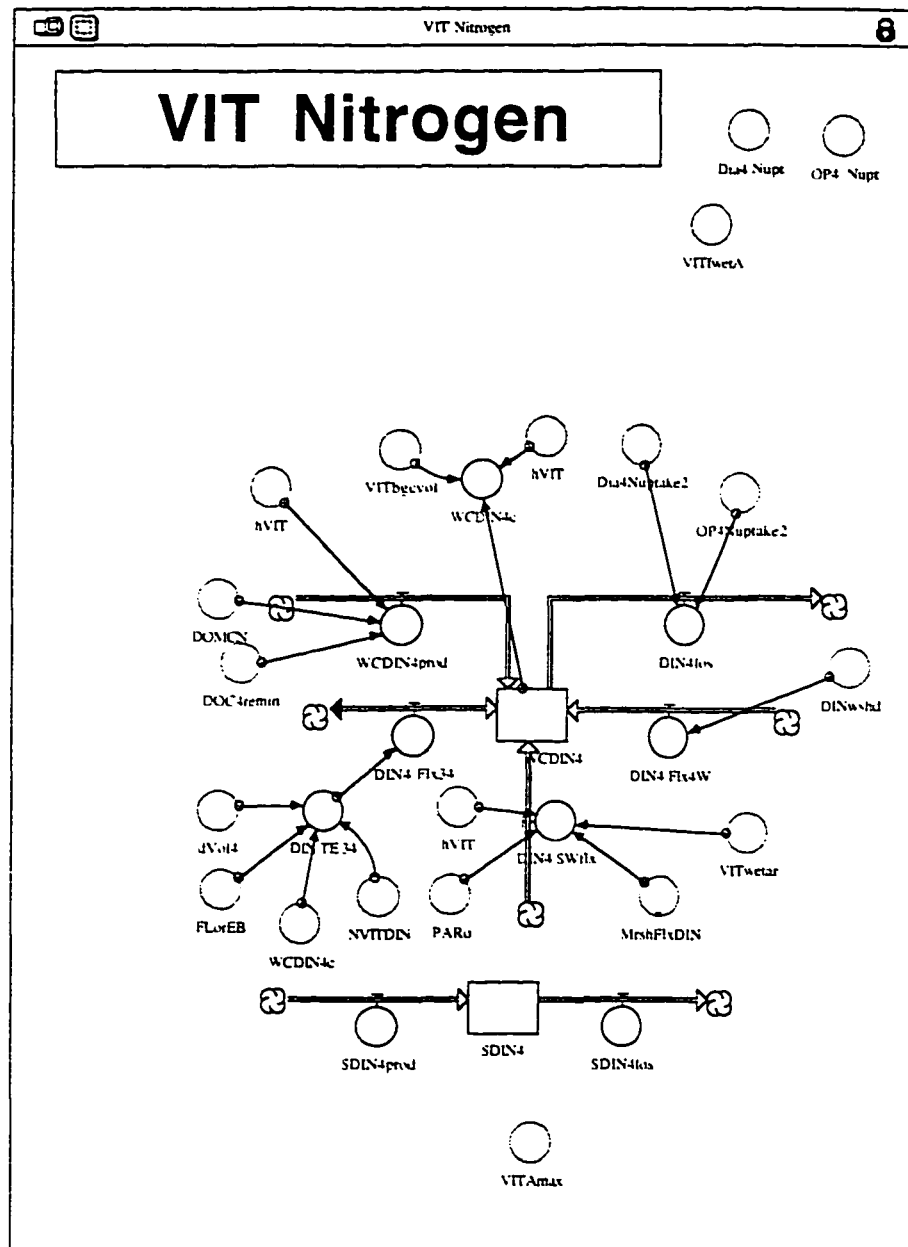




Spartina Integrators

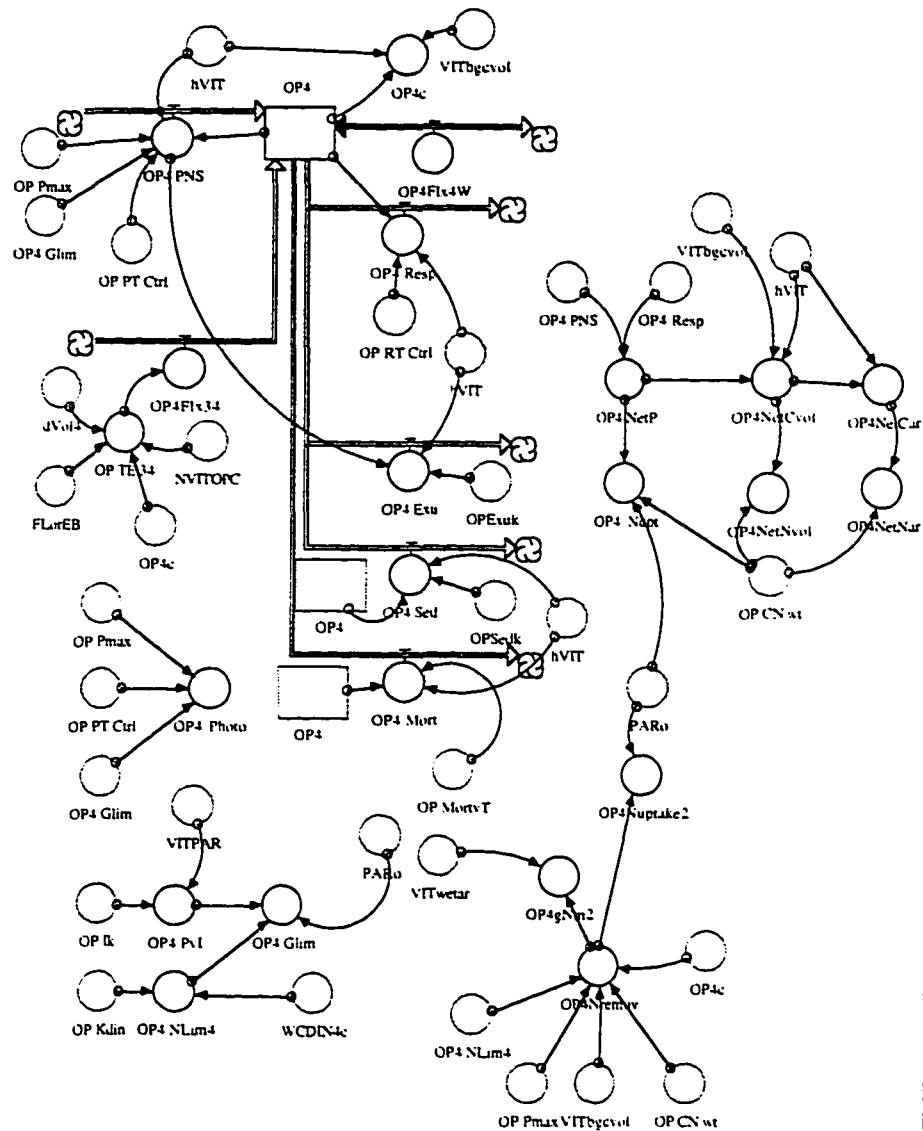


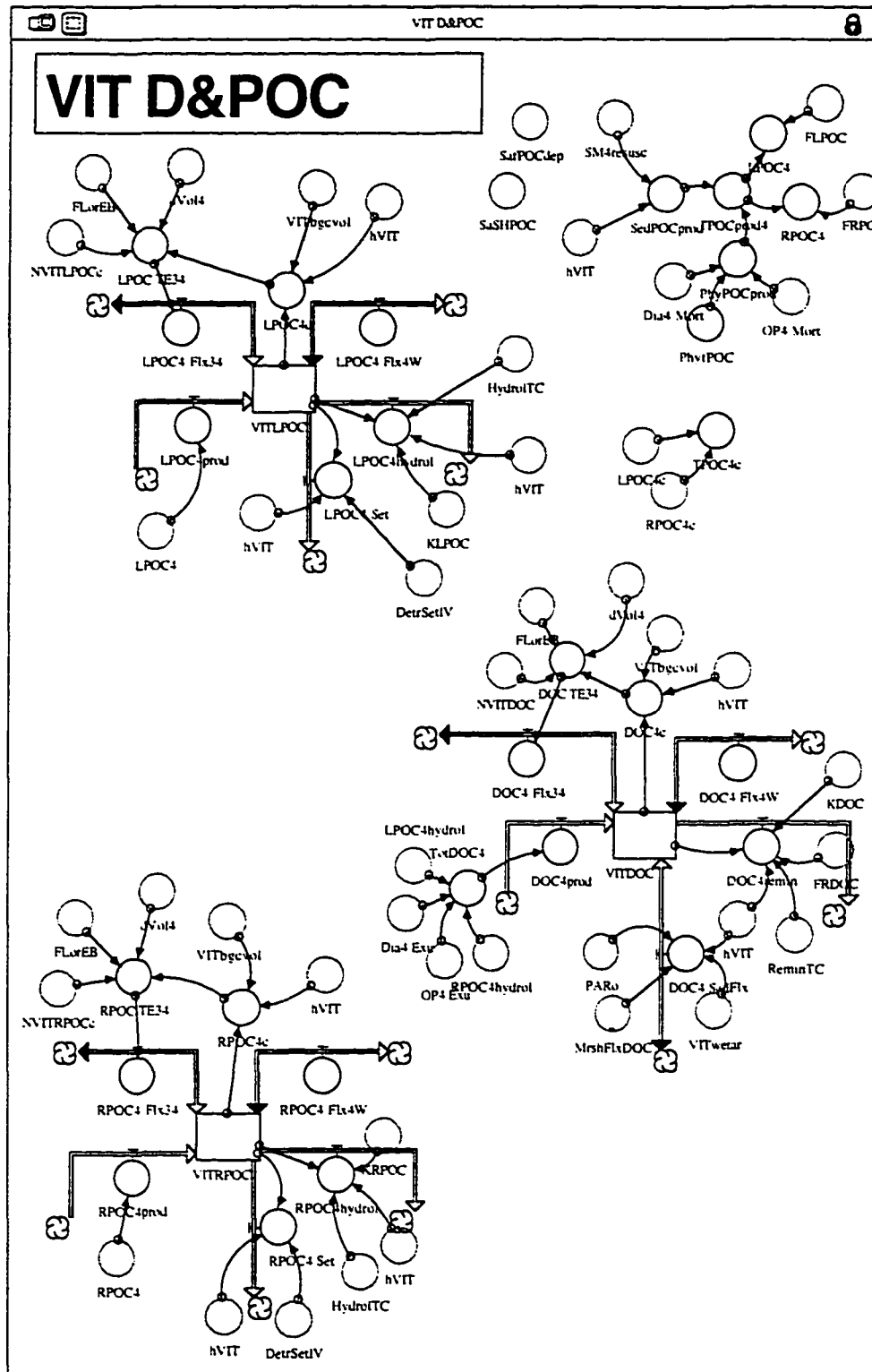


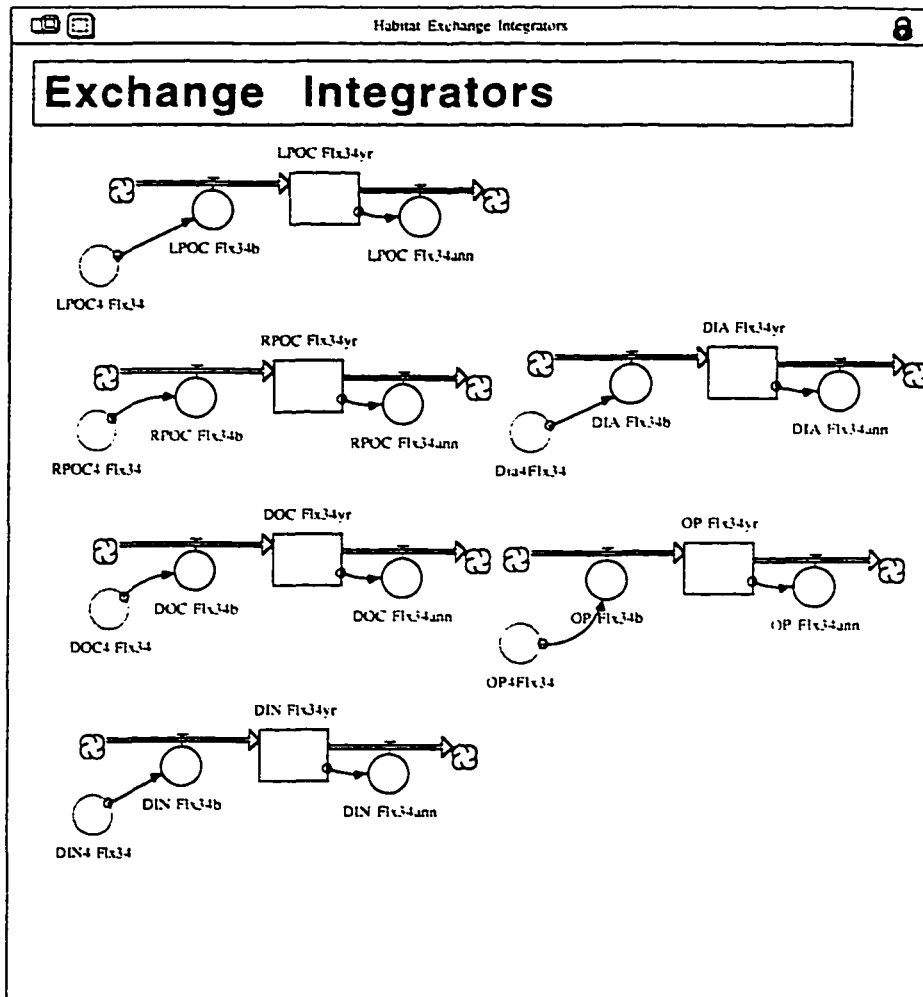


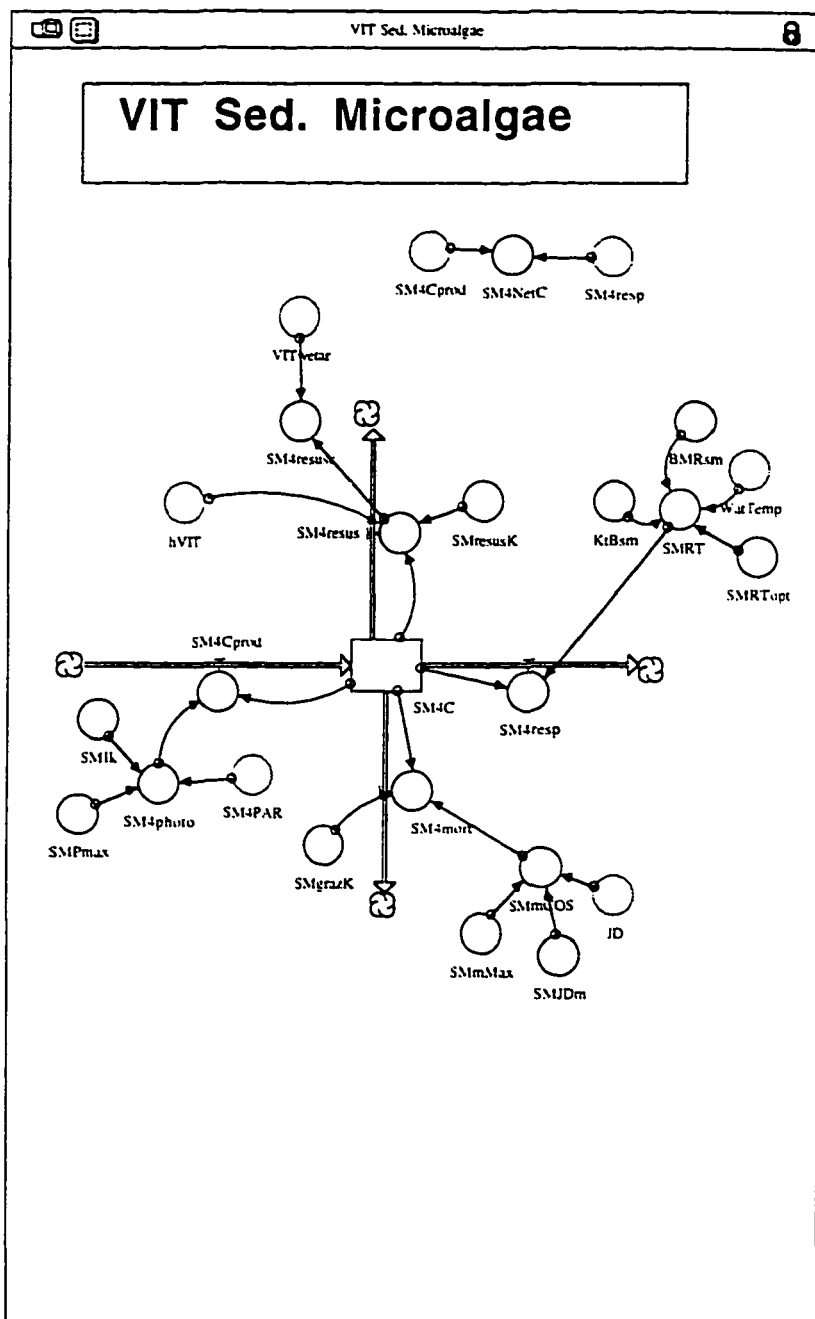
[illegible]

VIT Other Phytoplankton

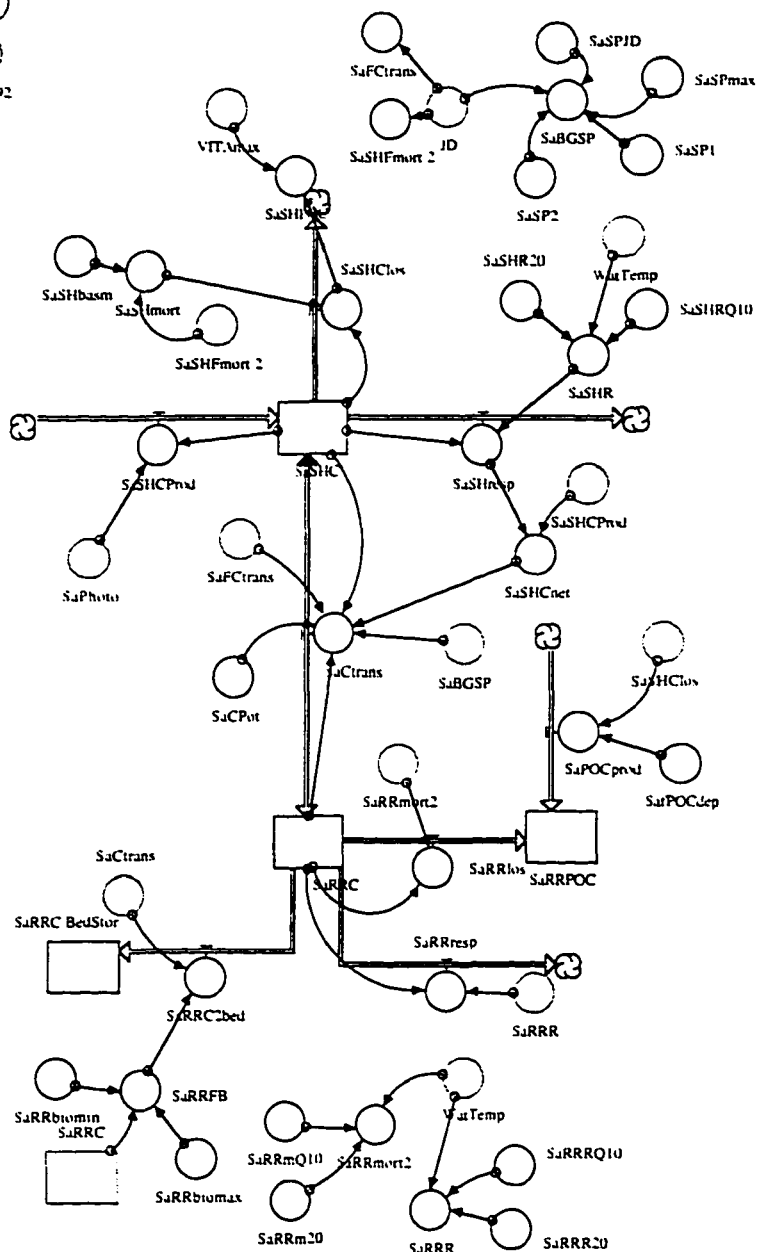








GPAT42



Vegetated Intertidal Habitat Model Equations

PHYTO AND SM C&N INTEGRATORS

$$\text{Dia4netCday}(t) = \text{Dia4netCday}(t - dt) + (\text{Dia4NetCar2} - \text{Dia4netC24hr}) * dt$$

INIT Dia4netCday = 0.0

DOCUMENT: Daily Diatom Productivity. (gC/m²/d) This accumulates (or loses?) net diatoms each DT and spits out daily values.

$$\text{Dia4NetCar2} = \text{Dia4NetCar}$$

DOCUMENT: Diatom Net C Production, VIT. (gC/m²/d).

$$\text{Dia4netC24hr} = \text{PULSE}(\text{Dia4netCday}, 2, 1)$$

DOCUMENT: Integrated Daily Diatom Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$$\text{Dia4NetCyr}(t) = \text{Dia4NetCyr}(t - dt) + (\text{Dia4NetCar3} - \text{Dia4netCann}) * dt$$

INIT Dia4NetCyr = 0.0

DOCUMENT: Annual Diatom Productivity. (gC/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$$\text{Dia4NetCar3} = \text{Dia4NetCar}$$

DOCUMENT: Diatom Net C Production, VIT. (gC/m²/d).

$$\text{Dia4netCann} = \text{PULSE}(\text{Dia4NetCyr}, 365, 365)$$

DOCUMENT: Integrated Annual Diatom Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$$\text{Dia4NetNyr}(t) = \text{Dia4NetNyr}(t - dt) + (\text{Dia4NetNar2} - \text{Dia4netNann}) * dt$$

INIT Dia4NetNyr = 0.0

DOCUMENT: Annual Diatom Productivity. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$$\text{Dia4NetNar2} = \text{Dia4NetNar}$$

DOCUMENT: Diatom Net N Production, VIT. (gN/m²/d).

$$\text{Dia4netNann} = \text{PULSE}(\text{Dia4NetNyr}, 365, 365)$$

DOCUMENT: Integrated Annual Diatom Net Production. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$$\text{Dia4Nremyr}(t) = \text{Dia4Nremyr}(t - dt) + (\text{Dia4Nremoval} - \text{Dia4NremAnn}) * dt$$

INIT Dia4Nremyr = 0.0

DOCUMENT: Annual Diatom N Removal. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$$\text{Dia4Nremoval} = \text{Dia4gNm2}$$

DOCUMENT: Diatom Net N Removal, VIT. (gN/m²/d).

$$\text{Dia4NremAnn} = \text{PULSE}(\text{Dia4Nremyr}, 365, 365)$$

DOCUMENT: Integrated Annual Diatom N Removal. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP1Nremyr(t) = OP1Nremyr(t - dt) + (OP1Nremoval2 - OP1NremAnn) * dt$

INIT $OP1Nremyr = 0.0$

DOCUMENT: Annual OP N Removal. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP1Nremoval2 = OP4gNm2$

DOCUMENT: OP Net N Removal, VIT. (gN/m²/d).

$OP1NremAnn = PULSE(OP1Nremyr, 365, 365)$

DOCUMENT: Integrated Annual OP N Removal. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP4NetCyr(t) = OP4NetCyr(t - dt) + (OP4NetCar3 - OP4netCann) * dt$

INIT $OP4NetCyr = 0.0$

DOCUMENT: Annual OP Productivity. (gC/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP4NetCar3 = OP4NetCar$

DOCUMENT: OP Net C Production, VIT. (gC/m²/d).

$OP4netCann = PULSE(OP4NetCyr, 365, 365)$

DOCUMENT: Integrated Annual OP Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP4NetNyr(t) = OP4NetNyr(t - dt) + (OP4NetNar3 - OP4netNann) * dt$

INIT $OP4NetNyr = 0.0$

DOCUMENT: Annual OP Productivity. (gN/m²/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP4NetNar3 = OP4NetNar$

DOCUMENT: OP Net N Production, VIT. (gN/m²/d).

$OP4netNann = PULSE(OP4NetNyr, 365, 365)$

DOCUMENT: Integrated Annual OP Net Production. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SM4netCday(t) = SM4netCday(t - dt) + (SM4netC2 - SM4netC24hr) * dt$

INIT $SM4netCday = 0.0$

DOCUMENT: Daily Sediment Microalgae Productivity. (gC/m²/d) This accumulates (or loses?) net Sediment Microalgae each DT and spits out daily values.

$SM4netC2 = SM4NetC$

DOCUMENT: Sediment Microalgae Net C Production, VIT. (gC/m²/d).

$SM4netC24hr = PULSE(SM4netCday, 2, 1)$

DOCUMENT: Integrated Daily Sediment Microalgae Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SM4netCyr(t) = SM4netCyr(t - dt) + (SM4netC3 - SM4netCann) * dt$

INIT $SM4netCyr = 0.0$

DOCUMENT: Annual Sediment Microalgae Productivity. (gC/m²/yr) This accumulates (or loses?) net

Sediment Microalgae each DT and spits out yearly values.

$SM4netC3 = SM4NetC$

DOCUMENT: Sediment Microalgae Net C Production. VIT. ($gC/m^2/d$).

$SM4netCann = PULSE(SM4netCyr, 365, 365)$

DOCUMENT: Integrated Annual Sediment Microalgae Net Production. ($gC/m^2/yr$). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

DATA

$DetrSetlV = 0.25$ {0.25 for VIT; WES=1.0}

DOCUMENT: Detritus Settling Velocity. (m/d). From Waterways Experiment Station.

$DINwshd = 0$

DOCUMENT: DIN Watershed. (μM). This is the value for DIN from the terrestrial boundary. Not in effect for Goodwin Islands.

$DOMCN = 10$

DOCUMENT: Dissolved Organic Matter C:N. (unitless). This is the C:N ratio of water column DOM.

$FLPOC = 0.55$

DOCUMENT: Fraction Labile POC. (unitless). 55% of total POC is labile. From Cerco&Cole.

$FRDOC = 0.0$

DOCUMENT: Fraction Refractory DOC. (unitless). This is the unusable fraction of the DOC. Set at 20% Refractory, 80% Labile upon suggestion from Mark Meyers.

$FRPOC = 0.45$

DOCUMENT: Fraction Refractory POC. (unitless). 45% of total POC is refractory. From Cerco&Cole.

$HydroITC = EXP(KHydrol*(WatTemp-TrHydol))$

DOCUMENT: Hydrolysis Temperature effect. (unitless). Exponential effect term.

$KDC = 0.01$

DOCUMENT: Constant for Labile Dissolved Carbon Remineralization. (/d). From Cerco & Cole, 1994. {0.01=1/day}

$KDOC = KDC$

DOCUMENT: Constant for Labile Dissolved Carbon Remineralization. (/d). From Cerco & Cole, 1994. Used if different than KDC.

$KHydrol = 0.069$

DOCUMENT: Constant for Hydrolysis (unitless?). From Cerco & Cole. Hydrolysis goes from POC to DOC

$KLC = 0.075$

DOCUMENT: Constant for Labile Carbon Hydrolysis to DOC. (/d). Cerco & Cole, 1994: 0.075 (15 d "e-folding" time). Changed to 0.00556, 180-d e-folding time scale. (e.g.: 30-d e-folding time [$e^{-(30*0.033)} = e^{-1} = 36.7\%$ of starting value]).

KLPOC = KLC

DOCUMENT: Constant for Labile Carbon Remineralization. (/d). From Cerco & Cole, 1994. Used if different from KLC.

KRC = 0.005

DOCUMENT: Constant for Refractory Particulate Carbon Hydrolysis to DOC. (/d). From Cerco & Cole, 1994.

KRemin = 0.069

DOCUMENT: Constant for Remineralization. (unitless?). From Cerco & Cole. Remineralization takes DOC and makes DON.

KRPOC = KRC

DOCUMENT: Constant for Refractory Particulate Carbon Remineralization. (/d). From Cerco & Cole, 1994. Used if different than KRC.

NVITDiaC = 0.165

DOCUMENT: NonVegetated Subtidal Diatom C Conc. (gC/m3). $10 \text{ mg Chla/m}^3 / 1000 * 50 \text{ gC/gChla} * 0.33 \text{ (fraction Diatoms)} = 0.165$

NVITDIN = 5.0

DOCUMENT: NonVegetated Intertidal Water Column DIN Conc. (mmoles/m3). 5 uM taken from Moore GI Intensive.

NVITDOC = 3.5

DOCUMENT: NonVegetated Subtidal DOC. (gC/m3). This is the NVIT (3) boundary DOC concentration for the VIT habitat (4). 2.5-11.8 mgC/L referenced in Williams et al. 1992, Bly Creek, SC. Betty recorded 3.5 gC/m3 at EShore.

NVITLPOCc = 5*FLPOC

DOCUMENT: Channel POC Concentration. (gC/m3). Monthly averaged AFDW from SAV Hab. Monit. Prgm's GM station, which is actually in the eelgrass habitat.

NVITOPC = 0.33

DOCUMENT: NonVegetated Subtidal Diatom C Conc. (gC/m3). $10 \text{ mg Chla/m}^3 / 1000 * 50 \text{ gC/gChla} * 0.67 \text{ (fraction Diatoms)} = 0.33$

NVITRPOCc = 5*FRPOC

OPtlPhyto = 0.67

DOCUMENT: Other Plankton:Total Phytoplankton ratio. (unitless). From Ray, Haas & Sieracki, 1989: Table 1. 67% over all size classes.

POM_CN = 10

DOCUMENT: Particulate Organic Matter C:N. (unitless). This is the C:N ratio of water column POM.

ReminTC = $\text{EXP}(\text{KRemin} * (\text{WatTemp} - \text{TrRemin}))$

DOCUMENT: Remineralization Temperature effect. (unitless). Exponential effect term.

TrHydol = 20.0

DOCUMENT: Reference Temperature for Remineralization. (degC).

TrRemin = 20.0

DOCUMENT: Reference Temperature for Remineralization. (degC).

WCDia_Cchl = 50

DOCUMENT: Water Column Diatom C:Chl ratio. (unitless).

GMAfdw = GRAPH(TIME)

(0.00, 2.24), (33.2, 2.77), (66.4, 2.46), (99.5, 1.91), (133, 2.01), (166, 3.01), (199, 4.22), (232, 3.18), (265, 3.32), (299, 2.61), (332, 2.21), (365, 1.88)

DOCUMENT: Shoal Survey Guinea Marsh AFDW. (gC/m3). The AFDW of suspended sediment collected biweekly in the lower York River, Guinea Marsh means from 1984-1992 (mgC/L = gC/m3).

MrshFlx DIN = GRAPH(TIME)

(0.00, -0.2), (33.2, -0.2), (66.4, -2.49), (99.5, -0.97), (133, -2.75), (166, -2.50), (199, -2.09), (232, -4.00), (265, -4.16), (299, -3.50), (332, -3.10), (365, -1.56)

DOCUMENT: Marsh Flux of DIN. (mmol/m2/d). This is from Betty Berry's MA thesis data from Brownsville Marsh, Eshore, VA.

MrshFlxDOC = GRAPH(TIME)

(0.00, 0.00), (33.2, 0.08), (66.4, -0.2), (99.5, -0.35), (133, -0.3), (166, -0.25), (199, -0.3), (232, -0.35), (265, -0.32), (299, -0.3), (332, -0.35), (365, -0.42)

sedDIN4 = GRAPH(TIME)

(1.00, 174), (2.00, 190), (3.00, 210), (4.00, 312), (5.00, 332), (6.00, 342), (7.00, 363), (8.00, 365), (9.00, 356), (10.0, 346), (11.0, 264), (12.0, 211)

DOCUMENT: Sediment DIN 4, VIT. (uM). Graph used until state variable is defined. Will become unit converter later.

ShoalAirTemp = GRAPH(time)

(0.00, 2.00), (33.2, 5.00), (66.4, 14.0), (99.5, 19.0), (133, 22.0), (166, 25.0), (199, 32.0), (232, 35.0), (265, 25.0), (299, 19.0), (332, 14.0), (365, 10.0)

DOCUMENT: Shoal Air Temperature. (degC). This graph is from actual data collected at Goodwin Islands during 1994. Should include multi-annual means, but now is only 1994.

PAR.TEMP,DEPTH

Declination = $0.39637 - 22.9133 \cdot \cos(\text{psi}) + 4.02543 \cdot \sin(\text{psi}) - 0.3872 \cdot \cos(2 \cdot \text{psi}) + 0.052 \cdot \sin(2 \cdot \text{psi})$

DOCUMENT: Solar declination. Used to define photoperiod for a given day and latitude. Kirk, 1994, p. 35. Psi is in radians.

deltaWL = tidal_wl-DELAY(tidal_wl,DT)

DOCUMENT: d Tidal Water Level. (m). This is the change in tidal wl over dt. DELAY delays the output of a value by a given time lag.

dVol4 = deltaWL*VITwetar

DOCUMENT: delta Volume 4, VIT. (m3). This calculates the change in volume each time step. DELAY delays the output of a value by a given time lag.

eps = 0.00 {"Near-Zero"}

DOCUMENT: eps. (m). I have no idea what eps stands for but it is a potential correction factor for deltaWL.

FLorEB = IF (deltaWL-eps > 0.0) THEN 1 ELSE IF (deltaWL-eps < 0.0) THEN -1 ELSE 0
DOCUMENT: Flood or Ebb. This switch determines if the tidal WL is increasing or decreasing.

GI_Hyps = 2.752E06 * tidal_wl + 9.375E05

DOCUMENT: GI Hypsometric Curve Predicts Wet Area. (m2). This is a linear fit of hypsometric data that ranges -0.35 to 0.35 m tidal height and 0 to 1.85E06 m2 wet area.

GloPtM2 = MSL+(0.363*COS(0.5059*modlhrs-4.365))

GIPTM2S2 = MSL+(0.363*COS(0.5059*modlhrs-4.365))+(0.067*COS(0.5236*modlhrs-5.0388))

DOCUMENT: Tidal water level. (m). This is total tide height from a combination of mean sea level and the first 2 harmonic components (M2 and S2) of the tidal equation for Gloucester Point, VA . Tide equation relative to Mean Low Water!

GIPTid93 = MSL+(0.356*COS(0.5059*modlhrs-1.583))+(0.067*COS(0.5236*modlhrs-5.0388))+(0.074*COS(0.4964*modlhrs+1.2636))+(0.047*COS(0.2625*modlhrs-1.8535))+(0.037*COS(0.2434*modlhrs+0.0332))

DOCUMENT: Tidal water level. (m). This is total tide height from a combination of mean sea level and the first 5 harmonic components of the tidal equation for Gloucester Point, VA. tidal year 1993 . Tide equation relative to Mean Low Water!

GIPTid95 = MSL+(0.363*COS(0.5059*modlhrs-4.365))+(0.067*COS(0.5236*modlhrs-5.0388))+(0.075*COS(0.4964*modlhrs+1.6685))+(0.044*COS(0.2625*modlhrs-1.9199))+(0.092*COS(0.0014*modlhrs+2.2811))+(0.098*COS(0.0007*modlhrs+2.0071))

DOCUMENT: Tidal water level. (m). This is total tide height from a combination of mean sea level and the first 6 harmonic components of the tidal equation for Gloucester Point, VA. Tidal year 1995 . Tide equation relative to Mean Low Water!

hfilm = 0.01

DOCUMENT: h film. (m). The thickness of the water layer over the intertidal habitats that is not exchanged. Used to prevent habitats from being totally dry.

hVIT = IF(tidal_wl>0.00)THEN(tidal_wl-zVIT)ELSE(0.0)

DOCUMENT: VIT Habitat depth. (m). This is the depth of the vegetated intertidal habitat + over the tidal cycle. The IF..THEN..ELSE is to assure that depth is never negative.

Insolation = 28.25 - 16.75*COS(2*PI*(JD+10)/365)

DOCUMENT: Incident solar irradiance (insolation) at Gloucester Point, VA in Einsteins/m2/day. Taken from Wetzel and Neckles (1986).

JD = IF Steady=0 THEN JDstart + INT(TIME) ELSE Jdstart

DOCUMENT: Julian Day. TIME is days but the integer is used to prevent rounding errors.

JDstart = 0

DOCUMENT: Julian Day to start. User can input starting day, otherwise model starts 1 January.

latitude = 38*(PI/180)

DOCUMENT: Latitude. (radians). User can input latitude in degrees, converted to radians. Lower Ches. Bay assumed to be 38N.

MaxIrradiance = 277.78*PI*Insolation/(2*photoperiod)

DOCUMENT: Maximum Daily Irradiance. (uEinsteins/m2/sec). This converter calculates the maximum

daily irradiance value from the total daily insolation.

$\text{modlhrs} = \text{TIME} * 24$

$\text{MSL} = 0.00$

DOCUMENT: Mean Sea Level. (m). This is h0 in the tidal equation and sets reference baseline for all elevations.

$\text{NVITAm} = 925000$

DOCUMENT: Maximum area of NVIT. (m²). This sets maximum area for habitat 3 when marsh is fully inundated.

$\text{PARo} = \text{MAX}(\text{MaxIrradiance} * \text{COS}(2 * \text{PI} * (\text{thours} - 12) / (2 * \text{photoperiod})), 0.0)$

DOCUMENT: Surface Downwelling PAR. (uE/m²/s). This is an hourly light curve formulated similar as that in Wetzel and Neckles (1986).

$\text{photoperiod} = 11.75 - 2.25 * \text{COS}(2 * \text{PI} * (\text{JD} + 10) / 365)$

DOCUMENT: Photoperiod function taken from Wetzel and Neckles (1986). Calculates photoperiod in hours/day.

$\text{psi} = \text{MOD}(\text{JD} - 1.365) / 365 * 2 * \text{PI}$

DOCUMENT: psi. (radians). Date of year expressed as an angle that provides the argument, in radians, for solar declination formula. $\text{MDAY} = \text{Model day}$, starting at day 1 on Jan 1. Kirk, 1983, p. 36.

$\text{sinB} = \text{SIN}(\text{latitude}) * \text{SIN}(\text{Declination} * \text{PI} / 180) - \text{COS}(\text{latitude}) * \text{COS}(\text{Declination} * \text{PI} / 180) * \text{COS}(\text{tau})$

DOCUMENT: sin B. (unitless). Solar elevation (solar angle) calculated according to JTO Kirk. For use in light attenuation due to plant biomass.

$\text{Steady} = 0$ {0/1: annual cycle or fixed day}

$\text{tau} = \text{thours} / 24 * 2 * \text{PI}$

DOCUMENT: Tau. (radians). Clock hour in degrees, converted to radians. From JTO Kirk.

$\text{thours} = \text{MOD}(\text{TIME}, 1) * 24$

DOCUMENT: Time in hours. This converter takes time in days and converts it to hours for use in physical forcing functions (i.e. tidal wl and PAR).

$\text{tidal_wl} = \text{GIPtTid93}$

DOCUMENT: Tidal water level. (m). This is total tide height from either the M2 only, the M2S2, or the top 6 components of the tidal equation for Gloucester Point, VA in 1993 or 1995. Tide equation relative to Mean Low Water!

$\text{VITAm} = 850000$

DOCUMENT: Maximum area of VIT. (m²). Used in the calculation of sediment biogeochemical stocks.

$\text{VITbgcvol} = (\text{hfilm} * \text{VITAm}) + \text{VITvol}$

DOCUMENT: VIT Biogeochemistry Volume. (m³). The permanent film volume plus the exchanged volume.

$\text{VITfwetA} = \text{VITwetar} / \text{VITAm}$

DOCUMENT: VIT Fractional Wet Area. (unitless ratio). This is the fraction VIT wet area is of the max. wet area.

VITvol = MAX(hVIT-hfilm,0.0)*VITwetar

DOCUMENT: Volume of VIT. (m3). This is the volume of the vegetated intertidal habitat 2 based upon the wet area * the habitat depth relative to msl and a fluctuating free surface. Hfilm maintains some water over the marsh surface.

VITwetar = IF(tidal_wl ≥ 0.0) AND (tidal_wl < 0.36)

THEN (GIIntWetArea_2-NVITAmx) ELSE IF(tidal_wl > 0.36)

THEN (VITAmx) ELSE (0.0)

DOCUMENT: Inundated area of VIT. (m2). This is the wetted area of the vegetated intertidal habitat 4. This value fluctuates with tidal water level.

WatTemp = 16.25-13.75*COS(2*PI*(JD-25)/365)

DOCUMENT: Water Temperature. (degC). This is a water temperature function for the York River, V.A. Taken from Wetzel and Neckles (1986).

zVIT = 0.0

DOCUMENT: Elevation of the VIT habitat 4. (m). This is the reference elevation for the vegetated intertidal habitat 4 relative to MSL. The minimum marsh elevation recorded at the Goodwin Islands using GPS = 0.05

GIIntWetArea = GRAPH(tidal_wl)

(-0.36, 0.00), (-0.309, 83000), (-0.257, 160000), (-0.206, 330000), (-0.154, 500000), (-0.103, 660000), (-0.0514, 830000), (4.16e-17, 1e+06), (0.0514, 1.2e+06), (0.103, 1.3e+06), (0.154, 1.4e+06), (0.206, 1.5e+06), (0.257, 1.6e+06), (0.309, 1.7e+06), (0.36, 1.8e+06)

DOCUMENT: GI Intertidal Wet Area. This is the intertidal wetted area (m2) derived using a drawn HC with a sigmoid shape. Tide ranges from 0-0.4 m and area ranges from 0 to 1E+06 m2.

GIIntWetArea_2 = GRAPH(tidal_wl)

(-0.55, 0.00), (-0.5, 84091), (-0.45, 168182), (-0.4, 252273), (-0.35, 336364), (-0.3, 420455), (-0.25, 504545), (-0.2, 588636), (-0.15, 672727), (-0.1, 756818), (-0.05, 840909), (-6.94e-17, 925000), (0.05, 1e+06), (0.1, 1.1e+06), (0.15, 1.2e+06), (0.2, 1.3e+06), (0.25, 1.3e+06), (0.3, 1.4e+06), (0.35, 1.5e+06), (0.4, 1.6e+06), (0.45, 1.7e+06), (0.5, 1.8e+06), (0.55, 1.8e+06)

DOCUMENT: GI Intertidal Wet Area. This is the intertidal wetted area (m2) derived using a drawn HC with a sigmoid shape. Tide ranges from 0-0.4 m and area ranges from 0 to 1E+06 m2.

HABITAT EXCHANGE INTEGRATORS

DIA_Flx34yr(t) = DIA_Flx34yr(t - dt) + (DIA_Flx34b - DIA_Flx34ann) * dt

INIT DIA_Flx34yr = 0.0

DOCUMENT: Annual DIA Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

DIA_Flx34b = Dia4Flx34

DOCUMENT: Diatom Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of diatoms between the NVIT & VIT habitats.

DIA_Flx34ann = PULSE(DIA_Flx34yr,365,365)

DOCUMENT: Integrated Annual DIA Exchange. (gC/m2/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

DIN_Flx34yr(t) = DIN_Flx34yr(t - dt) + (DIN_Flx34b - DIN_Flx34ann) * dt

INIT DIN_Flx34yr = 0.0

DOCUMENT: Annual DIN Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$DIN_Flx34b = DIN4_Flx34$

DOCUMENT: DIN Tidal Exchange between Habitats 3 & 4. (mmoles/d). The physical exchange of DIN between the NVIT and VIT habitats.

$DIN_Flx34ann = PULSE(DIN_Flx34yr, 365, 365)$

DOCUMENT: Integrated Annual DIN Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$DOC_Flx34yr(t) = DOC_Flx34yr(t - dt) + (DOC_Flx34b - DOC_Flx34ann) * dt$

INIT $DOC_Flx34yr = 0.0$

DOCUMENT: Annual DOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$DOC_Flx34b = DOC4_Flx34$

DOCUMENT: DOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of RPOC between the NVIT and VIT habitats.

$DOC_Flx34ann = PULSE(DOC_Flx34yr, 365, 365)$

DOCUMENT: Integrated Annual DOC Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$LPOC_Flx34yr(t) = LPOC_Flx34yr(t - dt) + (LPOC_Flx34b - LPOC_Flx34ann) * dt$

INIT $LPOC_Flx34yr = 0.0$

DOCUMENT: Annual LPOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$LPOC_Flx34b = LPOC4_Flx34$

DOCUMENT: LPOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of LPOC between the NVIT & VIT habitats.

$LPOC_Flx34ann = PULSE(LPOC_Flx34yr, 365, 365)$

DOCUMENT: Integrated Annual POC Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$OP_Flx34yr(t) = OP_Flx34yr(t - dt) + (OP_Flx34b - OP_Flx34ann) * dt$

INIT $OP_Flx34yr = 0.0$

DOCUMENT: Annual OP Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$OP_Flx34b = OP4Flx34$

DOCUMENT: Other Plankton Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of OP between the NVIT & VIT habitats.

$OP_Flx34ann = PULSE(OP_Flx34yr, 365, 365)$

DOCUMENT: Integrated Annual OP Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$RPOC_Flx34yr(t) = RPOC_Flx34yr(t - dt) + (RPOC_Flx34b - RPOC_Flx34ann) * dt$

INIT $RPOC_Flx34yr = 0.0$

DOCUMENT: Annual RPOC Exchange. (gC/yr) This accumulates (or loses?) net diatom each DT and spits out yearly values.

$RPOC_Flx34b = RPOC4_Flx34$

DOCUMENT: RPOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of RPOC between the NVIT and VIT habitats.

$RPOC_Flx34ann = PULSE(RPOC_Flx34yr, 365, 365)$

DOCUMENT: Integrated Annual POC Exchange. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

PLANKTON CONTROL

$BMRd = 0.01$

DOCUMENT: Diatom Basal Metabolic Rate. (/d). From WES Ches. Bay model (0.01/d in WES).

$BMRop = 0.01$

DOCUMENT: Other Plankton Basal Metabolic Rate. (/d). From WES Ches. Bay model (0.01/d in WES).

$Chl4 = 1000 * (Dia4c + OP4c) / WCDia_Cchl$

DOCUMENT: Chlorophyll Conc. 4, VIT. (mg/m³). This is the total phytoplankton mass converted to concentration and then to chlorophyll biomass using C:Chla=50.

$DiaExuk = 0.3$

DOCUMENT: Diatom Exudation Constant. 10% of Production is lost through exudation of DOC. Changed to 30% 5 Feb 96. Moloney&Field, 1991, used 15% for Benguela Current, SA.

$DiaPT1 = 0.004$

DOCUMENT: Diatom Photosynthesis Temp Coeff. 1. (/degC²). Used in Gaussian curve.

$DiaPT2 = 0.006$

DOCUMENT: Diatom Photosynthesis Temp Coeff. 2. (/degC²). Used in Gaussian curve.

$DiaSedk = 0.25$

{1E-09} DOCUMENT: Diatom Sedimentation Coefficient. (m/d). Park&Kuo used 0.35 (Jan-May) and 0.1 (June-Dec).

$Dia_CN_wt = 5.7$

DOCUMENT: Diatoms C:N Redfield Weight Ratio. 106:16 in weight units.

$Dia_Ik = 140$

DOCUMENT: Diatom Ik. (uE/m²/s). From Pax Shallow.

$Dia_Kdin = 10 \{uM\} DIN$

DOCUMENT: Diatom Ks DIN. The half sat. constant for DIN uptake by diatoms.

$Dia_MortvT = PRRd * EXP(KtBd * (WatTemp - Dia_RTopt))$

DOCUMENT: Diatom Mortality Temperature Control. (). This is the effect of temperature on diatom mortality.

Dia_Pmax = 1.0 {HPEL dia_Pmax=0.75; WES's Pd=2.25}

DOCUMENT: Diatom Pmax. (gC/gC/d).

Dia_PTopt = 20

DOCUMENT: Diatom Photosynthesis Optimal Temperature. (degC). Like most everything else, estimated @ 20.

Dia_PT_Ctrl = IF (WatTemp<=Dia_PTopt) THEN
(EXP(-DiaPT1*(WatTemp-Dia_PTopt)^2)) ELSE
(EXP(-DiaPT2*(Dia_PTopt-WatTemp)^2))

DOCUMENT: Diatom Photosynthesis Temperature Control. (unitless). This is the effect of temperature on diatom photosynthesis. CBWQ MODEL

Dia_RTopt = 20

DOCUMENT: Diatom Respiration Optimal Temperature. (degC).

Dia_RT_Ctrl = BMRd*EXP(KtBd*(WatTemp-Dia_RTopt))

DOCUMENT: Diatom Respiration Temperature Control. (). This is the effect of temperature on diatom respiration.

KtBd = 0.069

DOCUMENT: Diatom Respiration Temp Coeff. 1. (/degC). Used in exp. curve.

KtBop = 0.069

DOCUMENT: Other Plankton Photosynthesis Temp Coeff. 1. (/d). Used in exp. curve.

OPExuk = 0.3

DOCUMENT: Diatom Exudation Constant. 10% of Production is lost through exudation of DOC. Changed to 30% 5 Feb 96. Moloney&Field, 1991. used 15% for Benguela Current, SA.

OPSedk = 0.1

{1E-09}

DOCUMENT: Diatom Sedimentation Coefficient. (m/d). Park&Kuo used 0.1 m/d.

OP_CN_wt = 5.7

DOCUMENT: Other Plankton C:N Redfield Weight Ratio. 106:16 in weight units.

OP_Ik = 140

DOCUMENT: Other Plankton Ik. (uE/m2/s). From Pax Shallow.

OP_Kdin = 10 {uM DIN}

DOCUMENT: Other Plankton Ks DIN. The half sat. constant for DIN uptake by OP.

OP_MortvT = PRRop*EXP(KtBop*(WatTemp-OP_RTopt))

DOCUMENT: Other Plankton Mortality Temperature Control. (/d). This is the effect of temperature on other plankton mortality.

OP_Pmax = 1.0 {g C/g C/day; WES's Green algal Pg=2.5}

DOCUMENT: Other Plankton Pmax. (gC/gC/d).

OP_PT1 = 0.008

DOCUMENT: Other Plankton Photosynthesis Temp Coeff. 1. (/degC^2). Used in Gaussian curve.

OP_PT2 = 0.010

DOCUMENT: Other Plankton Photosynthesis Temp Coeff. 2. (/degC^2). Used in Gaussian curve.

OP_PTopt = 25.0

DOCUMENT: Other Plankton Photosynthesis Optimal Temperature. (degC).

OP_PT_Ctrl = IF (WatTemp<=OP_PTopt) THEN
(EXP(-OP_PT1*(WatTemp-OP_PTopt)^2)) ELSE
(EXP(-OP_PT2*(OP_PTopt-WatTemp)^2))

DOCUMENT: Other Plankton Photosynthesis Temperature Control. (unitless). This is the effect of temperature on other plankton photosynthesis.

OP_RTopt = 20

DOCUMENT: Other Plankton Respiration Optimal Temperature. (degC).

OP_RT_Ctrl = BMROP*EXP(KtBOP*(WatTemp-OP_RTopt))

DOCUMENT: Other Plankton Respiration Temperature Control. (/d). This is the effect of temperature on other plankton respiration.

Phy4area = PHYto4NetProd*hVIT

DOCUMENT: VIT Phytoplankton 4 Areal Net Production. (gC/m2/d). The volumetric net rate * the habitat depth.

PHYto4NetProd = Dia4NetCvol+OP4NetCvol

DOCUMENT: VIT Phytoplankton 4 Net Production. (gC/m3/d). The volumetric net productivity rate.

PRRd = 0.15

DOCUMENT: Diatom Basal Mortality Rate. (/d). From WES Ches. Bay model (0.215/d in Park&Kuo).

PRROp = 0.15

DOCUMENT: Other Plankton Basal Mortality Rate. (/d). From WES Ches. Bay model (0.215/d in Park&Kuo).

SMmortK = 0.05

DOCUMENT: Sediment Microalgal Mortality Coefficient. (/gC?). This is for a quadratic loss term suggested by M. Meyers (from Dominic Ditoro?).

SMNKs = 1.5

DOCUMENT: Sediment Microalgae N Ks. (uM). The half sat constant for N uptake by SM.

SMNVmax = 0.25

DOCUMENT: Sediment Microalgae N Vmax. (gN/gN/d). The max rate of N uptake by SM.

SPARTINA C&N INTEGRATORS

SaRRNdemyr(t) = SaRRNdemyr(t - dt) + (SaRRNdem2 - SRRNdemAnn) * dt

INIT SaRRNdemyr = 0

DOCUMENT: Annual Spartina RR N Demand. (gN/m2) This accumulates (or loses?) net RR each DT

and spits out annual values.

SaRRNdem2 = SaRRNdemand

DOCUMENT: Spartina RR Net Nitrogen Production. (gN/m²/d). The net production/C:N.

SRRNdemAnn = PULSE(SaRRNdemyr,365,365)

DOCUMENT: Integrated Yearly Spartina RR Nitrogen Demand. (gN/m²/d). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

SaRRnetCday(t) = SaRRnetCday(t - dt) + (SaRRCnet2 - SaRRnetC24) * dt

INIT SaRRnetCday = 0

DOCUMENT: Daily Spartina RR Productivity. (gC/m²) This accumulates (or loses?) net RR each DT and spits out daily values.

SaRRCnet2 = SaRRCnet

DOCUMENT: Spartina RR Net Carbon Production. (gC/m²/d). The sum of translocation, RR respiration, RR mortality, and RR C lost to bed storage.

SaRRnetC24 = PULSE(SaRRnetCday,24,24)

DOCUMENT: Integrated Daily Spartina RR Net Production. (gC/m²/d). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

SaRRnetCyr(t) = SaRRnetCyr(t - dt) + (SaRRCnet3 - SRRnetCann) * dt

INIT SaRRnetCyr = 0

DOCUMENT: Annual Spartina RR Productivity. (gC/m²) This accumulates (or loses?) net RR each DT and spits out annual values.

SaRRCnet3 = SaRRCnet

DOCUMENT: Spartina RR Net Carbon Production. (gC/m²/d). The sum of translocation, RR respiration, RR mortality, and RR C lost to bed storage.

SRRnetCann = PULSE(SaRRnetCyr,365,365)

DOCUMENT: Integrated Yearly Spartina RR Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

SaSHCday(t) = SaSHCday(t - dt) + (SaSHCnet2 - SaSHC24hr) * dt

INIT SaSHCday = 0.0

DOCUMENT: Daily Spartina Shoot Productivity. (gC/m²) This accumulates (or loses?) net Spartina productivity each DT and spits out daily values.

SaSHCnet2 = SaSHCnet

DOCUMENT: Spartina Shoot Net Carbon Production. (gC/m²/d). This is difference between gross P and respiration.

SaSHC24hr = PULSE(SaSHCday,2,1)

DOCUMENT: Integrated Daily Spartina Shoot Net Production. (gC/m²/day). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

SaSHCyr(t) = SaSHCyr(t - dt) + (SaSHCnet3 - SSnetCann) * dt

INIT SaSHCyr = 0.0

DOCUMENT: Annual Spartina Shoot Productivity. (gC/m²) This accumulates (or loses?) net Spartina

Shoot Prod each DT and spits out yearly values.

$SaSHCnet3 = SaSHCnet$

DOCUMENT: Spartina Shoot Net Carbon Production. (gC/m²/d). This is difference between gross P and respiration.

$SSnetCann = PULSE(SaSHCyr, 365, 365)$

DOCUMENT: Integrated Annual Spartina Shoot Net Production. (gC/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SRRNuptyr(t) = SRRNuptyr(t - dt) + (SaRRNupt2 - SRRNuptAnn) * dt$

INIT $SRRNuptyr = 0.0$

DOCUMENT: Annual Spartina RR N Uptaken. (gN/m²) This accumulates (or loses?) net Spartina Shoot Prod each DT and spits out yearly values.

$SaRRNupt2 = SaRRNupt$

DOCUMENT: Spartina alterniflora RR Nitrogen Uptake. (gN/m²/d).

$SRRNuptAnn = PULSE(SRRNuptyr, 365, 365)$

DOCUMENT: Integrated Annual Spartina RR N Uptake. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SSHNdemyr(t) = SSHNdemyr(t - dt) + (SaSHNdem2 - SSNdemAnn) * dt$

INIT $SSHNdemyr = 0.0$

DOCUMENT: Annual Spartina Shoot N Demand. (gN/m²) This accumulates (or loses?) net Spartina Shoot Prod each DT and spits out yearly values.

$SaSHNdem2 = SaSHNdemand$

DOCUMENT: Spartina alterniflora Shoot Nitrogen Demand. (gN/m²/d). Based upon net C production (gC/m²/d) and the optimal weight C:N=32.

$SSNdemAnn = PULSE(SSHNdemyr, 365, 365)$

DOCUMENT: Integrated Annual Spartina Shoot Net Production. (gN/m²/yr). This PULSE function identifies the volume to be accumulated, the time of the first pulse, and the pulse interval.

$SaRRCdaytot = SaRRnetC24 * VITAmay$

DOCUMENT: Spartina RR C daily total net. (gC/d). The areal rate * the habitat area.

$SaRRCyrtot = SRRnetCann * VITAmay$

DOCUMENT: Spartina RR C annual total net. (gC/yr). The areal rate * the habitat area.

$SaRRNdemand = SaRRCnet / SaRRCN$

DOCUMENT: Spartina RR Net Nitrogen Production. (gN/m²/d). The net production/C:N.

$SaSHCdaytot = SaSHC24hr * VITAmay$

DOCUMENT: Spartina Shoot C daily total net. (gC/d). The areal rate * the habitat area.

$SaSHCyrtot = SSnetCann * VITAmay$

DOCUMENT: Spartina Shoot C annual total net. (gC/yr). The areal rate * the habitat area.

VIT DOC & POC

$VITDOC(t) = VITDOC(t - dt) + (DOC4_{prod} + DOC4_{Flx34} + DOC4_{SedFlx} - DOC4_{remin} - DOC4_{Flx4W}) * dt$

INIT VITDOC = 0

DOCUMENT: DOC 4, VIT. (gC). This is the total DOC mass in g for the VIT habitat. Initialized at 0.0.

$DOC4_{prod} = TotDOC4$

DOCUMENT: Total DOC Production, VIT (gC/d).

$DOC4_{Flx34} = DOC_TE34$

DOCUMENT: DOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of DOC between the NVIT & VIT habitats.

$DOC4_{SedFlx} = IF(PARo > 0.0) AND(hVIT > 0.0) THEN(MrshFlxDOC * VITwetar)$

ELSE(0.0)

DOCUMENT: DOC + Sediment Water Flux, VIT. (gC/d). This is the mass exchange between the sediment and water.

$DOC4_{remin} = IF(hVIT > 0.0) THEN(KDOC * ReminTC * (1 - FRDOC) * VITDOC) ELSE(0.0)$

DOCUMENT: DOC + Remineralization, VIT. (gC/d). A function of the DOC, the remineralization term, and a remin. constant. Cerco & Cole, 1994.

$DOC4_{Flx4W} = 0$

DOCUMENT: DOC + Flux with Watershed. (gC/d). This is the exchange with the upland boundary. Set = 0.0 for the Goodwin Islands.

$VITLPOC(t) = VITLPOC(t - dt) + (LPOC4_{prod} + LPOC4_{Flx34} - LPOC4_{hydrol} - LPOC4_{Set} - LPOC4_{Flx4W}) * dt$

INIT VITLPOC = 0

DOCUMENT: LPOC 4, VIT. (gC). This is the total LPOC mass in g for the VIT habitat. Initialized at 0.0.

$LPOC4_{prod} = LPOC4$

DOCUMENT: Labile POC 4, NVIT. (gC/d). The total POC production * labile fraction (55% Cerco&Cole).

$LPOC4_{Flx34} = LPOC_TE34$

DOCUMENT: LPOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of LPOC between the NVIT & VIT habitats.

$LPOC4_{hydrol} = IF(hVIT > 0.0) THEN(KLPOC * HydroITC * VITLPOC) ELSE(0.0)$

DOCUMENT: POC Remineralization, VIT. (gC/d). A function of the POC, the remineralization term, and a remin. constant. Cerco & Cole, 1994.

$LPOC4_{Set} = IF(hVIT > 0.0) THEN(VITLPOC * DetrSetV/hVIT) ELSE(0.0)$

DOCUMENT: LPOC 4 Settling, VIT. (gC/d). This is the fraction of the water column LPOC pool that settles daily. Set = 0.0 is habitat is not inundated. Set to 2x the Detritus Settling Velocity because this is a marsh.

LPOC4_Flx4W = 0

DOCUMENT: LPOC 4 Flux with Watershed. (gC/d). This is the exchange with the upland boundary.
Set = 0.0 for the Goodwin Islands.

VITRPOC(t) = VITRPOC(t - dt) + (RPOC4prod + RPOC4_Flx34 - RPOC4hydrol - RPOC4_Set -
RPOC4_Flx4W) * dt

INIT VITRPOC = 0

DOCUMENT: RPOC 4, VIT. (gC). This is the total RPOC mass in g for the VIT habitat. Initialized at 0.0.

RPOC4prod = RPOC4

DOCUMENT: Refractory POC 4, NVIT. (gC/d). The total POC production * refractory fraction (45% Cerco&Cole).

RPOC4_Flx34 = RPOC_TE34

DOCUMENT: RPOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of RPOC between the NVIT & VIT habitats.

RPOC4hydrol = IF (hVIT>0.0) THEN (KRPOC*HydrolTC*VITRPOC) ELSE (0.0)

DOCUMENT: RPOC Hydrolysis, VIT. (gC/d). A function of the RPOC, the hydrolysis term, and a constant. Cerco & Cole, 1994.

RPOC4_Set = IF (hVIT>0.0) THEN (VITRPOC*DetrSetIV/hVIT) ELSE (0.0)

DOCUMENT: RPOC 4 Settling, VIT. (gC/d). This is the fraction of the water column RPOC pool that settles daily. Set = 0.0 is habitat is not inundated.

RPOC4_Flx4W = 0

DOCUMENT: RPOC 4 Flux with Watershed. (gC/d). This is the exchange with the upland boundary.
Set = 0.0 for the Goodwin Islands.

DOC4c = IF (hVIT>0.0) THEN (VITDOC/VITbgcvol) ELSE (0.0)

DOCUMENT: DOC Concentration 4, VIT. (gC/m3).

DOC_TE34 = IF (FLorEB > 0) THEN (dVol4*NVITDOC) ELSE

(IF (FLorEB < 0) THEN (dVol4*DOC4c)

ELSE (0.0))

DOCUMENT: DOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of DOC between the NVIT & VIT habitats.

LPOC4 = FLPOC*TPOCprod4

DOCUMENT: Labile POC 4, NVIT. (gC/d). The total POC production * labile fraction (55% Cerco&Cole).

LPOC4c = IF (hVIT>0.0) THEN (VITLPOC/VITbgcvol) ELSE (0.0)

DOCUMENT: LPOC Concentration 4, VIT. (gC/m3). Set=0.0 when the habitat is not inundated.

LPOC_TE34 = IF (FLorEB > 0) THEN (dVol4*NVITLPOCc) ELSE

(IF (FLorEB < 0) THEN (dVol4*LPOC4c)

ELSE (0.0))

DOCUMENT: LPOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of LPOC between the NVIT & VIT habitats.

PhyfPOC = 0.8

DOCUMENT: POC Production Switch. (unitless). This is to set the fraction of plankton biomass that enters the WC POC pool.

PhyPOCprod = PhyfPOC*(Dia4_Mort+OP4_Mort)

DOCUMENT: Phytoplankton POC Production. (gC/d). This is to set the fraction of plankton biomass that enters the WC POC pool. We think most phyto biomass goes to zooplankton biomass and not to WC POC.

RPOC4 = FRPOC*TPOCprod4

DOCUMENT: Refractory POC 4, NVIT. (gC/d). The total POC production * refractory fraction (35% Cerco&Cole).

RPOC4c = IF (hVIT>0.0) THEN (VITRPOC/VITbgcvol) ELSE (0.0)

DOCUMENT: RPOC Concentration 4, VIT. (gC/m3). Set=0.0 when the habitat is not inundated.

RPOC_TE34 = IF (FLorEB > 0) THEN (dVol4*NVITRPOCc) ELSE

(IF (FLorEB < 0) THEN (dVol4*RPOC4c)

ELSE (0.0))

DOCUMENT: RPOC Tidal Exchange between Habitats 3 & 4. (gC/d). The physical exchange of RPOC between the NVIT & VIT habitats.

SedPOCprod = IF (hVIT>0.0) THEN (SM4resusc) ELSE (0.0)

TotDOC4 = Dia4_Exu+LPOC4hydrol+OP4_Exu+RPOC4hydrol

DOCUMENT: Total DOC Production, VIT (gC/d).

TPOC4c = LPOC4c+RPOC4c

TPOCprod4 = PhyPOCprod+SedPOCprod

DOCUMENT: Total Water Column POC Production Habitat 4, VIT. (gC/d). The sum of diatoms, other plankton, sediment microalgae, and a fraction of Spartina biomass.

VIT DIATOMS

Dia4(t) = Dia4(t - dt) + (Dia4_PNS + Dia4Flx34 - Dia4_Resp - Dia4_Mort - Dia4_Sed - Dia4_Exu - Dia4Flx4W) * dt

INIT Dia4 = 0

DOCUMENT: Diatom 4 mass, VIT. (gC). $10 * 0.33 * 50/1000 * 850000 \text{ m}^2 * 0.19\text{m} = 26648$

INIT=0.0 when model starts with tidalWL<0.0.

Dia4_PNS = IF(hVIT>0.0) THEN(Dia_Pmax*Dia_PT_Ctrl*Dia4_Glim * Dia4) ELSE(0.0)

DOCUMENT: Diatom 4 Production, VIT. (gC/d). From Pmax, temp control, growth limitation, and diatom biomass

Dia4Flx34 = Dia_TE_34

Dia4_Resp = IF(hVIT>0.0) THEN(Dia4*Dia_RT_Ctrl) ELSE(0.0)

DOCUMENT: Diatom 4 Respiration, VIT. (gC/d). A function of the respiratory coeff. and the resp. temp. control.

Dia4_Mort = IF(hVIT>0.0) THEN(Dia_MortvT*Dia4) ELSE(0.0)

DOCUMENT: Diatom 4 Mortality, VIT. (gC/d). This is loss to mortality from the mort. coeff. and the

diatom mass.

$\text{Dia4_Sed} = \text{IF}(\text{hVIT} > 0.0) \text{ THEN}(\text{DiaSedk} * \text{Dia4/hVIT}) \text{ ELSE}(0.0)$

DOCUMENT: Diatom + Sedimentation, VIT. (gC/d).

$\text{Dia4_Exu} = \text{IF}(\text{hVIT} > 0.0) \text{ THEN}(\text{DiaExuk} * \text{Dia4_PNS}) \text{ ELSE}(0.0)$

DOCUMENT: Diatom biomass +, VIT. (gC). INIT : 10 mg/m3 chl * 50 C:chl * 0.33 Dia:Ttl chl /1000 * MSL vol

$\text{Dia4Flx4W} = 0$

DOCUMENT: Diatom + (VIT) flux to Watershed. (gC/d). This is set to zero for the Goodwin Islands. No flux of plankton to watershed.

$\text{Dia4c} = \text{IF}(\text{hVIT} > 0.0) \text{ THEN}(\text{Dia4/VITbgcvol}) \text{ ELSE}(0.0)$

DOCUMENT: Diatom Concentration +, VIT. (gC/m3). This is the diatom concentration in the VIT habitat. Dia4 is in mass units, conc. is 0.0 when the habitat is not inundated.

$\text{Dia4gNm2} = \text{IF}(\text{VITwetar} > 0.0) \text{ THEN} (\text{Dia4Nremov} * 14/1000/\text{VITwetar}) \text{ ELSE} (0)$

DOCUMENT: Dia + N removal gN/m2/d.

$\text{Dia4NetCar} = \text{Dia4NetCvol} * \text{hVIT}$

DOCUMENT: Diatom + Net C by area (gC/m2/d). The volumetric rate * the depth.

$\text{Dia4NetCvol} = \text{IF}(\text{hVIT} > 0.0) \text{ THEN}(\text{Dia4_NetP}/\text{VITbgcvol}) \text{ ELSE}(0.0)$

DOCUMENT: Diatom + Net Production, VIT. (gC/m3/d). This is areal net prod=grosP-resp.

$\text{Dia4NetNar} = \text{Dia4NetCar}/\text{Dia_CN_wt}$

DOCUMENT: Diatom + Net N demand by area (gC/m2/d). The volumetric rate * the depth.

$\text{Dia4NetNvol} = \text{Dia4NetCvol}/\text{Dia_CN_wt}$

DOCUMENT: Diatom Net N Demand by Volume (gN/m3/d).

$\text{Dia4Nremov} = \text{Dia_Pmax} * \text{Dia4_NLim} * 1000 * \text{Dia4c}/14/\text{Dia_CN_wt} * \text{VITbgcvol}$

DOCUMENT: Diatom + Nitrogen Removal Equation (mmoleN/d).

$\text{NLim} * \text{Vmax}/\text{C:N} * \text{Biomass}/14 * 1000 * \text{VITvol}$ to convert from gN/gN/d to mmoleN/d.

$\text{Dia4Nuptake2} = \text{IF}(\text{PARo} > 0.0) \text{ THEN} (\text{Dia4Nremov}) \text{ ELSE} (0.0)$

$\text{Dia4_Glim} = \text{IF} (\text{PARo} > 0.0)$

$\text{THEN} (\text{IF} (\text{Dia4_NLim} > \text{Dia4_PvI}) \text{ THEN} (\text{Dia4_NLim}) \text{ ELSE} (\text{Dia4_PvI}))$

$\text{ELSE} (0.0)$

DOCUMENT: Diatom + Growth Limitation, VST. (unitless) Chooses between light and nutrient limitation.

$\text{Dia4_NetP} = \text{Dia4_PNS} - \text{Dia4_Resp}$

DOCUMENT: Diatom + Net Production, VIT. (gC/d). This is net prod=grosP-resp.

$\text{Dia4_NLim} = \text{WCDIN4c}/(\text{Dia_Kdin} + \text{WCDIN4c})$

DOCUMENT: Diatom + Nitrogen limitation, VIT. (unitless). This the hyperbolic tangent curve.

$\text{Dia4_Nupt} = \text{IF}(\text{PARo} > 0.0) \text{ THEN}(\text{Dia4_NetP} / \text{Dia_CN_wt} * 1000 / 14)$

$\text{ELSE}(0.0)$

DOCUMENT: Diatom + Nitrogen Uptake, VIT. (mmoleN/d). This is the net production converted to N using the Redfield C:N.

$\text{Dia4_Photo} = \text{Dia_Pmax} * \text{Dia_PT_Ctrl} * \text{Dia4_Glim}$

DOCUMENT: Diatom + Photosynthesis, VIT. (gC/gC/d). This is the specific diatom photo. function.

$\text{Dia4_PvI} = \text{VITPAR} / (\text{Dia_Ik} + \text{VITPAR})$

DOCUMENT: Diatom + Pvs I curve, VIT. (unitless). The standard hyperbolic tangent curve.

$\text{Dia_TE_34} = \text{IF} (\text{FLorEB} > 0) \text{ THEN } (\text{dVol4} * \text{NVITDiaC}) \text{ ELSE}$

$(\text{IF} (\text{FLorEB} < 0) \text{ THEN } (\text{dVol4} * \text{Dia4c})$

$\text{ELSE } (0.0))$

DOCUMENT: Diatom Tidal Exchange Hab 4. (gC/d). This is the physical tidal exchange of diatom mass between the NVIT boundary (3) and habitat 4 (VIT).

VIT LIGHT

$a_{\text{Sa}} = 0.002$

DOCUMENT: a. (m²/gC). Canopy light extinction measured by Morris (1989) to be 0.002 and borrowed from Pinkney & Zingmark 1993. This value was determined experimentally for *Spartina alterniflora*.

$\text{DOCatn} = 0.14$

DOCUMENT: PAR attenuation due to dissolved organic matter. (m²/gC). MacPherson & Miller estimated 21% of total K_d from DOC. I assumed K_{total} = 1.0 and DOC = 1.5 gC/m³ to derive 0.14.

$\text{KdDOC} = \text{DOC4c} * \text{DOCatn}$

$\text{KdPhy} = \text{Chl4} * \text{Phyatn}$

$\text{KdPOC} = \text{POCatn} * \text{TPOC4c}$

$\text{Kdwater} = 0.04$

DOCUMENT: PAR K attenuation due to water. (/m).

$\text{Kd_switch} = 2$

DOCUMENT: K_d switch. (unitless). Switch used to determine method of calculation for submarine light attenuation. 0=fixed, constant K_d. 1=data driven variable K_d. 2=compute K_d from individual factors.

$\text{Kttl} = \text{IF} (\text{hVIT} > 0.0) \text{ THEN } (\text{Kdwater} + \text{KdPOC} + \text{KdDOC} + \text{KdPhy})$

$\text{ELSE} (0.0)$

DOCUMENT: Vegetated Intertidal K_{Total}. (/m²). The combination of 4 water column K_d's that operate when the marsh is inundated.

$\text{Phyatn} = 0.0138$

DOCUMENT: PAR K attenuation due to Phytoplankton. (m²/mgChl). From MacPherson & Miller (1987).

$\text{POCatn} = 0.14$

DOCUMENT: PAR attenuation due to Particulate organic matter. (m²/gC). MacPherson & Miller estimated 72% of total K_d from DOC. I assumed K_{total} = 1.0 and POC = 5 gC/m³ to derive 0.14.

$\text{SM4PAR} = \text{IF} (\sin B > 0.0) \text{ THEN } (\text{VITPAR_2} * \text{EXP}(-a_{\text{Sa}} * \text{SaSHC} / \sin B)) \text{ ELSE } (0.0)$

DOCUMENT: Sediment Microalgae PAR, VST. (uE/m2/s). This is the PAR that reaches the sediment surface in the VST after being attenuated by depth and Zostera biomass. Prob. will change when PAR attenuation due to phytoplankton is entered.

VITKd = IF(Kd_switch=0) THEN (1.5) ELSE (IF(Kd_switch=1.5) THEN (1.0) ELSE (Kttl))

DOCUMENT: Vegetated Intertidal Downwelling Attenuation Coefficient. This value of 1.5/m is an initial guess to get the model going.

VITPAR = PARo*EXP(-VITKd*0.5*hVIT)

DOCUMENT: Vegetated Intertidal PAR. (uE/m2/s) This is the depth variable submarine light based upon downwelling attenuation. The 0.5 is an attempt to predict light at mid-depth.

VITPAR_2 = PARo*EXP(-VITKd*0.5*hVIT)

DOCUMENT: Vegetated Intertidal PAR. (uE/m2/s) This is the depth variable submarine light based upon downwelling attenuation.

VIT NITROGEN

SDIN4(t) = SDIN4(t - dt) + (SDIN4prod - SDIN4los) * dt

INIT SDIN4 = 1.05E7

DOCUMENT: Sediment Nitrogen DIN 2, VST. (mmoles). Nitrogen mass in upper 10 cm of VST sediments. 150 uM * 0.10 m * 700,000 m2.

SDIN4prod = 0

DOCUMENT: Sediment DIN 4 production, VIT. (mmoles/d). Production due to remineralization.

SDIN4los = 0.0

DOCUMENT: Sediment DIN 4 loss, VIT. (mmoles/d). This is the loss term for sediment DIN 4 due to uptake by phototrophs.

WCDIN4(t) = WCDIN4(t - dt) + (WCDIN4prod + DIN4_Flx34 + DIN4_Flx4W + DIN4_SWflx - DIN4los) * dt

INIT WCDIN4 = 0

DOCUMENT: Water Column DIN, VIT. (mmoles). This is initialized for the winter, lower Chesapeake Bay. Init. Mass = 3 uM=3.0 mmoles/m3 * 70,000 m3=210,000 mmoles (Average Vol). Set @ 0.0 because model starts on ebbing tide.

WCDIN4prod = IF (hVIT>0.0) THEN (DOC4remin/DOMCN/14*1000) ELSE(0.0)

DOCUMENT: Water Column DIN 4 production. (mmolesN/d). This is the water column remineralization term.

DIN4_Flx34 = DIN_TE_34

DOCUMENT: WCDIN Tidal Exchange Hab 4. (gC/d). This is the physical tidal exchange of WC DIN between the NVIT boundary (3) and habitat 4 (VIT).

DIN4_Flx4W = DINwshd*0.0

DOCUMENT: DIN 4 (VIT) flux to Watershed. (gC/d). This is set to zero for the Goodwin Islands. No flux of DIN with watershed.

DIN4_SWflx = IF(PARo>0.0) AND(hVIT>0.0) THEN(MrshFlxDIN*VITwetar) ELSE(0.0)

DOCUMENT: DIN4 Sediment-Water Flux. (mmole/d). The MarshFlx DIN from Betty Berry's thesis* wetarea. The flux is 0.0 at night.

$DIN4los = Dia4Nuptake2 + OP4Nuptake2$

DOCUMENT: Water Column DIN 4 loss, VIT. (mmoles/d). This is the water column DIN loss term to N uptake by phototrophs.

$DIN_TE_34 = IF (F_{LorEB} > 0) THEN (dVol4 * NVITDIN) ELSE$
 $IF (F_{LorEB} < 0) THEN (dVol4 * WCDIN4c)$
 $ELSE (0.0)$

DOCUMENT: WCDIN Tidal Exchange Hab 4. (gC/d). This is the physical tidal exchange of WC DIN between the NVIT boundary (3) and habitat 4 (VIT).

$WCDIN4c = IF (hVIT > 0.0) THEN (WCDIN4/VITbgcvol) ELSE (0.0)$

VIT OTHER PLANKTON

$OP4(t) = OP4(t - dt) + (OP4_PNS + OP4Flx34 - OP4_Resp - OP4_Mort - OP4_Sed - OP4_Exu -$
 $OP4Flx4W) * dt$
 $INIT\ OP4 = 0$

DOCUMENT: Other Plankton 4 mass, VIT. (gC). $10 * 0.66 * 50/1000 * 850000\ m^2 * 0.19m = 53295$
 $INIT=0.0$ when model starts with tidalWL<0.0

$OP4_PNS = IF (hVIT > 0.0) THEN (OP_Pmax * OP_PT_Ctrl * OP4_Glim * OP4) ELSE (0.0)$

DOCUMENT: Other Plankton 4 Production. (gC/d). From Pmax, temp control, growth limitation, and diatom biomass. Equal to 0.0 when marsh is not inundated.

$OP4Flx34 = OP_TE_34$

DOCUMENT: OP Tidal Exchange Hab 4. (gC/d). This is the physical tidal exchange of OP mass between the NVIT boundary (3) and habitat 4 (VIT).

$OP4_Resp = IF (hVIT > 0.0) THEN (OP4 * OP_RT_Ctrl) ELSE (0.0)$

DOCUMENT: Other Plankton 4 Respiration, VIT. (gC/d). A function of the respiratory coeff. and the resp. temp. control.

$OP4_Mort = IF (hVIT > 0.0) THEN (OP_MortvT * OP4) ELSE (0.0)$

DOCUMENT: Other Plankton 4 Mortality, VIT. (gC/d). This is loss to mortality from the mort. coeff. and the OP mass.

$OP4_Sed = IF (hVIT > 0.0) THEN (OPSedk * OP4/hVIT) ELSE (0.0)$

DOCUMENT: Other Plankton 4 Sedimentation, VIT. (gC/d).

$OP4_Exu = IF (hVIT > 0.0) THEN (OPExuk * OP4_PNS) ELSE (0.0)$

DOCUMENT: Other Plankton 4 Exudation, VIT. (gC/d). This is a fraction of OP production.

$OP4Flx4W = 0$

DOCUMENT: Other Plankton 4 (VIT) flux to Watershed. (gC/d). This is set to zero for the Goodwin Islands. No flux of plankton to watershed.

$OP4c = IF (hVIT > 0.0) THEN (OP4/VITbgcvol) ELSE (0.0)$

DOCUMENT: Other Plankton Concentration 4, VIT. (gC/m3). This is the other plankton concentration

in the VIT habitat. OPhyto4 is in mass units, conc. is 0.0 when the habitat is not inundated.

OP4gNm2 = IF(VITwetar>0.0) THEN (OP4Nremov*14/1000/VITwetar) ELSE (0)

DOCUMENT: OP 4 N removal gN/m2/d.

OP4NetCar = OP4NetCvol*hVIT

DOCUMENT: OP 4 Net C by area (gC/m2/d). The volumetric rate * the depth.

OP4NetCvol = IF(hVIT>0.0) THEN (OP4_NetP/VITbgcvol) ELSE(0.0)

DOCUMENT: Other Plankton 4 Net Production, VIT. (gC/m3/d). This is volumetric net prod=grosP-resp.

OP4NetNar = OP4NetCar/OP_CN_wt

DOCUMENT: OP 4 Net N demand by area (gC/m2/d). The volumetric rate * the depth.

OP4NetNvol = OP4NetCvol/OP_CN_wt

DOCUMENT: Other Plankton Net N Demand by Volume (gN/m3/d).

OP4Nremov = OP_Pmax*OP4_NLim4*1000*OP4c/14/OP_CN_wt*VITbgcvol

DOCUMENT: OP 4 Nitrogen Removal Equation (mmoleN/d).

NLim4*Vmax/C:N*Biomass/14*1000*VITvol to convert from gN/gN/d to mmoleN/d.

OP4Nuptake2 = IF(PARo>0.0) THEN (OP4Nremov) ELSE (0.0)

OP4_Glim = IF (PARo > 0.0)

THEN (IF (OP4_NLim4>OP4_PvI) THEN (OP4_NLim4) ELSE (OP4_PvI))

ELSE (0.0)

DOCUMENT: Other Plankton 4 Growth Limitation, VIT. (unitless)? Chooses between light and nutrient limitation.

IF PARo > 0.0

THEN IF (OP4_NLim4>OP4_PvI) THEN OP4_NLim4 ELSE OP4_PvI

ELSE 0.0

OP4_NetP = OP4_PNS-OP4_Resp

DOCUMENT: Other Plankton 4 Net Production, VIT. (gC/d). This is net prod=grosP-resp.

OP4_NLim4 = WCDIN4c/(OP_Kdin+WCDIN4c)

DOCUMENT: Other Plankton 4 Nitrogen limitation, VIT. (unitless). This the hyperbolic tangent curve.

OP4_Photo = OP_Pmax*OP_PT_Ctrl*OP4_Glim

DOCUMENT: Other Plankton 4 Photosynthesis, VIT. (gC/gC/d). This is the specific diatom photo. function.

OP4_PvI = VITPAR/(OP_Ik+VITPAR)

DOCUMENT: Other Plankton 4 Pvs I curve, VIT. (unitless). The standard hyperbolic tangent curve.

OP4__Nupt = IF(PARo>0.0) THEN(OP4_NetP / OP_CN_wt * 1000 / 14)

ELSE(0.0)

DOCUMENT: Other Plankton 4 Nitrogen Uptake, VIT. (mmoleN/d). This is the net production converted to N using the Redfield C:N.

OP_TE_34 = IF (FLorEB > 0) THEN (dVol4 * NVITOPC) ELSE

(IF (FLorEB < 0) THEN (dVol4 * OP4c)

ELSE (0.0))

DOCUMENT: OP Tidal Exchange Hab 4. (gC/d). This is the physical tidal exchange of OP mass between the NVIT boundary (3) and habitat 4 (VIT).

VIT SEDIMENT MICROALGAE

$SM4C(t) = SM4C(t - dt) + (SM4Cprod - SM4resp - SM4mort - SM4resus) * dt$

INIT SM4C = 2.0

DOCUMENT: Sediment Microalgae Carbon, VIT. (gC/m2). The value of 55 mgChla/m2 was converted by multiplying by 50:1 C:Chla and converted to grams to derive 2.7 gC/m2. 2.0 is final value of stable model runs??

$SM4Cprod = SM4C * SM4photo$

DOCUMENT: Sediment Microalgae Gross C Production, VIT. (gC/m2/d).

$SM4resp = SM4C * SMRT$

DOCUMENT: Sediment Microalgae Respiration, VIT. (gC/m2/d). Respiration term for SM.

$SM4mort = (SMgrazK * SM4C^2) + (SM4C * SMmCOS)$

DOCUMENT: Sediment Microalgae Mortality, VIT. (gC/m2/d). This is a quadratic loss term suggested by M. Meyers (from Dominic Ditoro?).

$SM4resus = IF(hVIT > 0.0) THEN(SM4C * SMresusK) ELSE(0.0)$

DOCUMENT: Sediment Microalgae Resuspension, VIT. (gC/m2/d). This is a constant fraction of biomass lost to resuspension (Pinkney, pers. comm.).

$BMRsm = 0.05$

DOCUMENT: Diatom Respiration Temp Coeff. 2. (/d). Used in exp. curve. 0.01/d given in Cerco&Cole.

$KtBsm = 0.069$

DOCUMENT: Diatom Respiration Temp Coeff. 1. (/degC). Used in exp. curve.

$SM4NetC = SM4Cprod - SM4resp$

DOCUMENT: Sediment Microalgae Net C Production, VIT. (gC/m2/d).

$SM4photo = SMPmax * SM4PAR / (SMIk + SM4PAR)$

DOCUMENT: Sediment Microalgae Photosynthesis, VIT. (gC/gC/d). This is the hyperbolic tangent P vs I for SM.

$SM4resusc = SM4resus * VITwetar$

DOCUMENT: Sediment Microalgae Resuspension 4, VIT. (gC/d). This is the constant fraction of biomass lost to resuspension (gC/m2/d) multiplied by area (m2) in order to add to water column POC pool.

$SMgrazK = 0.045$

DOCUMENT: Sediment Microalgal Mortality Coefficient. (m2/gC/d). This is for a quadratic loss term suggested by M. Meyers (from Dominic Ditoro?).

$SMIk = 100$

DOCUMENT: Sediment Microalgae Ik, VST. (uE/m2/s). 1/2 sat. constant for BM photosynthesis. Calculated from Pinkney&Zingmark 1993. (Pmax=200 umolO2/mgChla/hr. . 0.576/d) to be ca 400.

Seems a bit high for our region. Pinkney, pers. comm. also.

SMJDm = 45

SMmCOS = MAX((0-(SMmMax* COS(2*PI*((JD+SMJDm)/365)))),0.0)

SMmMax = 0.05

SMPmax = 0.576

DOCUMENT: Sediment Microalgae Pmax. (gC/gC/d). The value of 200 umoleO2/mgchl_a/hr (Pinkney & Zingmark 1993) was converted assuming 50:1=C:Chl_a, C:O=1.0, and 12 hr daylength.

SMresusK = 0.05

DOCUMENT: Sediment Microalgal Resuspension Konstant. (unitless). 5% per day is guess by way of J Pinckney.

SMRT = BMRsm*EXP(KtBsm*(WatTemp-SMRTopt))

DOCUMENT: Sed Micalgae Respiration Temperature Control. (/d). This is the effect of temperature on sm respiration.

SMRTopt = 20

DOCUMENT: Diatom Respiration Optimal Temperature. (degC).

VIT SPARTINA ALTERNIFLORA

SaRRC(t) = SaRRC(t - dt) + (SaCtrans - SaRRresp - SaRRlos - SaRRC2bed) * dt

INIT SaRRC = 635

DOCUMENT: Spartina alterniflora RR Carbon. (gC/m²). The values of 7500 gdw/m² (total BG bio), 0.2 (20% live), and 0.35 gC/gdw were used to calc. the value of 525 gC/m². 635 is ending value for stable model runs??

SaCtrans = (SaCPot*SaSHCnet)+(SaBGSP*SaRRC)+(SaFCtrans*SaSHC)

DOCUMENT: Spartina alterniflora Carbon translocation. (gC/m²/d).

SaRRresp = SaRRC*SaRRR

DOCUMENT: Spartina alterniflora RR respiration. (gC/m²/d). Based upon Arrhenius expression.

SaRRlos = SaRRmort²*SaRRC

DOCUMENT: Spartina alterniflora RR Carbon Loss. (gC/m²/d).

SaRRC2bed = IF (SaRRFB = 1.0) THEN (max(SaCtrans,0.0)) ELSE (0.075*max(SaCtrans,0.0))

DOCUMENT: Spartina alterniflora RR Carbon to Bed Store. (gC/m²/d). When the RR C pool is at the maximum the whole amount of translocation is sent to the bed store, otherwise 10% of the trans. C is sent.

SaRRC_BedStor(t) = SaRRC_BedStor(t - dt) + (SaRRC2bed) * dt

INIT SaRRC_BedStor = 2100

DOCUMENT: Spartina alterniflora RR C Bed Store. (gC/m²). This is Spalt community bed C store. Initialized using 7500 gdw/m², 0.8 (80% dead), and 0.35 gC/gdw.

SaRRC2bed = IF (SaRRFB = 1.0) THEN (max(SaCtrans,0.0)) ELSE (0.075*max(SaCtrans,0.0))

DOCUMENT: Spartina alterniflora RR Carbon to Bed Store. (gC/m²/d). When the RR C pool is at the maximum the whole amount of translocation is sent to the bed store, otherwise 10% of the trans. C is sent.

SaRRN(t) = SaRRN(t - dt) + (SaRRNupt - SaNtrans - SaRRNlos - SaRRN2bed) * dt

INIT SaRRN = 6.5

DOCUMENT: *Spartina alterniflora* RR Nitrogen. (gN/m²). Initial value of 7.5 represents 525 gC/m² and a C:Nmin of 70 gC/gN (Hopkinson&Schubauer). 6.5 is ending value of stable model runs??

$$SaRRNupt = SaRRN * SaRRNmm$$

DOCUMENT: *Spartina alterniflora* RR Nitrogen Uptake. (gN/m²/d).

$$SaNtrans = SaSHNdemand * (1 - SRRCNFB) * (SSCNFB)$$

DOCUMENT: *Spartina alterniflora* Nitrogen translocation. (gN/m²/d). This is acropetal (RR to Shoot) N translocation. Inhibited when RR nitrogen becomes limiting.

$$SaRRNlos = SaRRlos / SaRRC * SaRRN$$

DOCUMENT: *Spartina alterniflora* RR Nitrogen Loss. (gN/m²/hr). This is Spalt RR nitrogen loss via RR mortality consistent with RR C loss.

$$SaRRN2bed = SaRRC2bed / SaRRoptCN$$

DOCUMENT: *Spartina alterniflora* RR Carbon to Bed Store. (gN/m²/d). This is Spalt RR nitrogen loss to bed storage consistent with RR carbon loss.

$$SaRRNBed(t) = SaRRNBed(t - dt) + (SaRRN2bed) * dt$$

$$INIT SaRRNBed = 30$$

DOCUMENT: *Spartina alterniflora* RR N Bed Store. (gN/m²). Spalt community bed N store initialized using 7500 gdw/m², 0.8 (80% dead), and 0.005 gN/gdw.

$$SaRRN2bed = SaRRC2bed / SaRRoptCN$$

DOCUMENT: *Spartina alterniflora* RR Carbon to Bed Store. (gN/m²/d). This is Spalt RR nitrogen loss to bed storage consistent with RR carbon loss.

$$SaRRPOC(t) = SaRRPOC(t - dt) + (SaRRlos + SaPOCprod) * dt$$

$$INIT SaRRPOC = 0$$

DOCUMENT: *Spartina alterniflora* RR POC. (gC/m²). This is the sediment POC pool that Spalt RR carbon feeds proportional with Shoot loss to POC.

$$SaRRlos = SaRRmort2 * SaRRC$$

DOCUMENT: *Spartina alterniflora* RR Carbon Loss. (gC/m²/d).

$$SaPOCprod = SaSHClos * SaPOCdep$$

DOCUMENT: *Spartina alterniflora* POC production. (gC/m²/d). In this case just the fraction of shoot POC that is retained in the marsh.

$$SaRRPON(t) = SaRRPON(t - dt) + (SaRRNlos) * dt$$

$$INIT SaRRPON = 0$$

DOCUMENT: *Spartina alterniflora* RR PON. gN/m². This is the PON pool that Sa RR N via mortality feeds. Initialized at 0.0.

$$SaRRNlos = SaRRlos / SaRRC * SaRRN$$

DOCUMENT: *Spartina alterniflora* RR Nitrogen Loss. (gN/m²/hr). This is Spalt RR nitrogen loss via RR mortality consistent with RR C loss.

$$SaSHC(t) = SaSHC(t - dt) + (SaSHCProd - SaSHresp - SaCtrans - SaSHClos) * dt$$

$$INIT SaSHC = 3$$

DOCUMENT: *Spartina alterniflora* Shoot Carbon. (gC/m²). This is the Shoot carbon for Spalt initialized for January.

$SaSHCProd = SaSHC * SaPhoto$

DOCUMENT: *Spartina alterniflora* Shoot Carbon Production. ($gC/m^2/d$). Spalt shoot gross C production.

$SaSHresp = SaSHC * SaSHR$

DOCUMENT: *Spartina alterniflora* Shoot Respiration. ($gC/m^2/d$).

$SaCtrans = (SaCPot * SaSHCnet) + (SaBGSP * SaRRC) + (SaFCtrans * SaSHC)$

DOCUMENT: *Spartina alterniflora* Carbon translocation. ($gC/m^2/d$).

$SaSHClos = SaSHmort * SaSHC$

DOCUMENT: *Spartina alterniflora* Shoot Carbon Loss. ($gC/m^2/d$).

$SaSHN(t) = SaSHN(t - dt) + (SaNtrans - SaSHNlos) * dt$

INIT $SaSHN = 0.3$

DOCUMENT: *Spartina alterniflora* Shoot Nitrogen. (gN/m^2). The initial value is from 10 gC/m^2 and the $SaSHminC:N$ of 17. 0.3 is ending value of stable model runs??

$SaNtrans = SaSHNdemand * (1 - SRRCNFB) * (SSCNFB)$

DOCUMENT: *Spartina alterniflora* Nitrogen translocation. ($gN/m^2/d$). This is acropetal (RR to Shoot) N translocation. Inhibited when RR nitrogen becomes limiting.

$SaSHNlos = SaSHClos / SaSHC * SaSHN$

DOCUMENT: *Spartina alterniflora* Shoot N mortality. ($gN/m^2/d$). This is shoot nitrogen loss as a fraction consistent with shoot C loss.

$SaSHPON(t) = SaSHPON(t - dt) + (SaSHNlos) * dt$

INIT $SaSHPON = 0$

DOCUMENT: *Spartina alterniflora* Shoot PON. (gN/m^2). This is the PON pool that Spalt Shoot N loss feeds.

$SaSHNlos = SaSHClos / SaSHC * SaSHN$

DOCUMENT: *Spartina alterniflora* Shoot N mortality. ($gN/m^2/d$). This is shoot nitrogen loss as a fraction consistent with shoot C loss.

$SaBGSP = -SaSPmax * (IF (MOD(JD,365) <= SaSPJD) THEN (EXP(-SaSP1 * (MOD(JD,365) - SaSPJD)^2)) ELSE (EXP(-SaSP2 * (SaSPJD - MOD(JD,365))^2)))$

DOCUMENT: *Spartina alterniflora* BG Spring Pulse. ($gC/gC/d$). This function provides a belowground spurt of C to the shoots around JD 115.

$SaCgdw = 0.43$

DOCUMENT: *Spartina alterniflora* Carbon per GDW. A value of 0.43 gC/gdw was cited in Morris et al. 1984. *Spartina alterniflora* Shoot Carbon content. (fraction of dw). Value of 0.32 gC/gdw shoots taken from IC Anderson Eshore data.

$SaCPot = 0.75$

DOCUMENT: *Spartina alterniflora* Carbon Translocation Potential. This sets the fraction of net production available for downward translocation. Taken from Morris, Houghton, & Botkin, 1984.

$SaFCtrans = MAX((0 - (0.0075 * COS(2 * PI * ((JD + 190) / 365)))) , 0.0)$

DOCUMENT: *Spartina alterniflora* Fall Translocation. ($gC/gC/d$). This function translocates a quantity of shoot carbon downwards to the RR during the fall senescing period.

(old value: 0.0816) {0.015*(IF (MOD(JD,365)<=SaJDt) THEN (EXP(-SaSHm1*(MOD(JD,365)-SaJDt)^2)) ELSE (EXP(-SaSHm2*(SaJDt-MOD(JD,365))^2)))}

SaPOCdep = 0.9

DOCUMENT: *Spartina alterniflora* Fraction POC deposited. (unitless). 90% of the Spalt Shoot POC stays in the VIT habitat. Only 10% transported.

SaIk = 265

DOCUMENT: *Spartina alterniflora* Ik. (uE/m²/s). Half-saturation constant for Spalt photosynthesis. Estimated from Pezeshki et al. 1987.

SaJDm = 365

DOCUMENT: *Spartina alterniflora* Julian Day Mort. This is the day of the year Spalt shoot mortality begins. Initially set for the fall equinox, day 270.

SaJDt = 365

SaPhoto = SaPmax * SaPTf * Sa_Glim

DOCUMENT: *Spartina alterniflora* Photosynthesis. (gC/gC/d). Pmax * Growth Limitation (chooses between I and sedN) * PT function.

SaPmax = 0.15

DOCUMENT: *Spartina alterniflora* Pmax. (gC/gC/d). This is from 0.02/hr * 12 hrs.

SaPTf = (IF(WarTemp<=SaTopt)THEN(EXP(-SaTk1*(WarTemp-SaTopt)^2))ELSE(EXP(-SaTk2*(SaTopt-WarTemp)^2)))

DOCUMENT: *Spartina alterniflora* Gross Production w Temperature. (unitless). This is a Gaussian function for temp vs gross production.

SaPvI = PARo/(SaIk+PARo)

DOCUMENT: *Spartina alterniflora* Photosynthesis. unitless. This is a hyperbolic tangent function (P vs I) for Spalt.

SaRRbiomax = 1000

DOCUMENT: *Spartina alterniflora* RR maximum biomass. This value was calculated using Goodwin Islands data 12.000 (gdw/m²) * 0.2(80%dead) * 0.4(gC/gdw). gC/m²

SaRRbiomin = 500

DOCUMENT: *Spartina alterniflora* RR. {limit. RR biomass concentration (gC/m²) above which density dependent factors could be in effect. }

SaRRCN = SaRRC/SaRRN

DOCUMENT: *Spartina alterniflora* RR C:N. This is the actual variable RR C:N from the model. weight ratio.

SaRRCnet = SaCtrans-SaRRresp

DOCUMENT: *Spartina alterniflora* RR Carbon net. (gC/m²/d). The translocated carbon minus the resp term.

$SaRRFB = \text{MIN}(\text{MAX}(SaRRC - SaRRbiomin, 0) / (SaRRbiomax - SaRRbiomin), 1.0)$

DOCUMENT: *Spartina alterniflora* RR Feedback. This is the Wiegert-Wetzel feedback function for basipetal translocation and RR production.

$SaRRKsN = 100$

DOCUMENT: *Spartina alterniflora* RR Ks Nitrogen. (μM). Set at 100 (like *Zostera*) because 5 μM seemed ridiculous. { This is the 1/2 sat. constant from Bradley&Morris 1990 for Michaelis-Menten uptake kinetics. }

$SaRRm20 = 0.0006$

DOCUMENT: *Spartina alterniflora* RR Mortality at 20degC. (gC/gC/d). This is the RR loss rate at the optimum temperature for use in an Arrhenius function.

$SaRRmaxCN = 300$

DOCUMENT: *Spartina alterniflora* RR maximum C:N. (molar ratio). This is the max. C:N WEIGHT RATIO for Sa RR. I assumed 0.4gC/gdw and 0.004gN/gdw. Also calculated from Hopkinson&Schubauer.

$SaRRminCN = 80$

DOCUMENT: *Spartina alterniflora* RR minimum C:N. (unitless weight ratio). Calculated from Ornes & Kaplan (1989).

$SaRRmort2 = SaRRm20 * SaRRmQ10^{(WatTemp - 20)}$

DOCUMENT: *Spartina alterniflora* RR Mortality. (gC/gC/d). This is the specific Sa RR mortality Arrhenius function.

$SaRRmQ10 = 1.25$

DOCUMENT: *Spartina alterniflora* RR Q10 value for mortality. This is the Q10 for use in the calculation of RR loss to sediment POC.

$SaRRNmax = 7.0$

DOCUMENT: *Spartina alterniflora* RR maximum Nitrogen. (gN/m^2) This value is from Fig 2 of Hopkinson & Schubauer (1984). Spalt from Georgia.

$SaRRNmin = 2.0$

DOCUMENT: *Spartina alterniflora* RR minimum Nitrogen. (gN/m^2) This value is from Fig 2 of Hopkinson & Schubauer (1984) Spalt from Georgia and calculated from Smith, Good, and Good (1979).

$SaRRNmm = (SRRCNFB) * SaSHRelGro * (SaRRVmN * SaRRVvS)$

DOCUMENT: *Spartina alterniflora* RR Nitrogen Uptake. (gN/gN/d). This function includes a Michaelis-Menten component, the RR N standing stock, a relative growth function that denies uptake during night, and a feedback function to limit N uptake as RR N content reaches max.

$SaRRoptCN = 200$

DOCUMENT: *Spartina alterniflora* Optimal C:N. (unitless weight ratio). Calculated from Smith, Good, and Good (1979).

$SaRRR = SaRRR20 * SaRRRQ10^{(WatTemp - 20)}$

DOCUMENT: *Spartina alterniflora* RR Respiration. (gC/gC/d). This is the specific Sa RR resp. Arrhenius function.

SaRRR20 = 0.0006

DOCUMENT: Spartina alterniflora RR Respiration at 20degC. (gC/gC/d). This is the RR resp. rate at the optimum temperature for use in an Arrenius function. { was 0.0012 but was too high, accounted for ca 80% of C trans }

SaRRRQ10 = 1.25

DOCUMENT: Spartina alterniflora RR Q10 value. This is the Q10 for use in the calculation of RR respiration.

SaRRVmN = 0.134

DOCUMENT: Spartina alterniflora RR Vmax. (gN/gN/d). The value of 8 umolN/gdwRoot/hr provided in Bradley & Morris 90 was converted to using 0.01gN/gdw and a 12 hour day = 0.134/d.

Note: Another Bradley&Morris (Ecology, 90) provides ca 13 umol/g/h. which derives 0.03 gN/gN/h.

SaRRVvS = sedDIN4/(SaRRKsN+sedDIN4)

DOCUMENT: Spartina alterniflora RR V vs S (unitless). Part of the Michaelis-Menten equation. Used as growth limiting factor.

SaSHbasM = 0.00375

DOCUMENT: Spartina alterniflora Shoot Basal Mortality. (gC/gC/d). This is the basal mortality coeff.

SaSHCN = SaSHC/SaSHN

DOCUMENT: Spartina alterniflora Shoot C:N. This is the actual variable shoot C:N from the model. weight ratio.

SaSHCnet = SaSHCProd-SaSHresp

SaSHCNopt = 32

DOCUMENT: Spartina alterniflora Shoot C:N optimal. (weight ratio). From 0.4 gC/gdw and 0.0125 gN/gdw. also average derived using Hopkinson & Schubauer data.

SaSHFmort_2 = MAX((0-(0.045* COS(2*PI*((JD+190)/365))))),0.0)

DOCUMENT: Spartina alterniflora Shoot fall Mort. (gC/gC/d). This is the maximum mortality rate function for fall shoot loss. { }

SaSHm1 = 0.0003

DOCUMENT: Spartina alterniflora Shoot Mort 1. This is a constant in the Spalt shoot loss equation.

SaSHm2 = 0.0005

DOCUMENT: Spartina alterniflora Shoot Mort 2. This is a constant in the Spalt shoot loss equation.

SaSHmaxCN = 30

DOCUMENT: Spartina alterniflora maximum C:N. weight ratio. Derived from Hopkinson & Schubauer (1984, 1984). Value for June.

SaSHminCN = 20

DOCUMENT: Spartina alterniflora minimum C:N. weight ratio. Derived from Hopkinson & Schubauer (1984, 1984) and Ornes and Kaplan (1989).

SaSHmort = SaSHbasM+SaSHFmort_2

DOCUMENT: Spartina alterniflora Shoot Mortality. (gC/gC/d). This is a Gaussian function for shoot mortality that initiates mortality at JD 270.

$SaSHNdemand = (SaSHCProd - SaSHresp) / SaSHCNopt$

DOCUMENT: *Spartina alterniflora* Shoot Nitrogen Demand. (gN/m²/d). Based upon net C production (gC/m²/d) and the optimal weight C:N=32.

$SaSHNmax = 5.5$

DOCUMENT: *Spartina alterniflora* Shoot maximum Nitrogen. (gN/m²) This value is from Fig 2 of Hopkinson & Schubauer (1984). Spalt from Georgia.

$SaSHPOC = SaSHClos * VITAmx$

DOCUMENT: *Spartina alterniflora* Shoot POC. (gC/d). Total POC from Spalt.

$SaSHR = SaSHR20 * SaSHRQ10^{(WatTemp - 20)}$

DOCUMENT: *Spartina alterniflora* Shoot Respiration. (gC/gC/d). This is the specific *Sa* shoot resp. Arrhenius function.

$SaSHR20 = 0.01325$

DOCUMENT: *Spartina alterniflora* Shoot Respiration at 20degC. (gC/gC/d). This is the shoot resp. rate at the optimum temperature for use in an Arrhenius function. { was 0.0045, too high net prod., tried 0.0075, tried 0.009 }

$SaSHRelGro = SaPhoto / SaPmax$

DOCUMENT: *Spartina alterniflora* Shoot Relative Growth. This is the fraction shoot photo is of Pmax. Each rate in gC/gC/hr. the ratio is unitless.

$SaSHRQ10 = 1.07$

DOCUMENT: *Spartina alterniflora* Shoot Q10 value. This is the Q10 for use in the calculation of shoot respiration.

$SaSP1 = 0.025$

DOCUMENT: *Spartina alterniflora* Spring Pulse factor 1. A factor for use in the sprpulse equation.

$SaSP2 = 0.025$

DOCUMENT: *Spartina alterniflora* Spring Pulse factor 2. A factor for use in the sprpulse equation.

$SaSPJD = 115$

DOCUMENT: *Spartina alterniflora* Spring Pulse Julian Day. Day 115 is the day shoots receive a belowground pulse of carbon.

$SaSPmax = 0.01$

{0.0042} DOCUMENT: *Spartina alterniflora* Maximum Spring Pulse. (gC/gC/d). This is the maximum rate of belowground carbon pulsed to the shoots on day 115.

$SaTk1 = 0.005$

DOCUMENT: *Spartina alterniflora* Temperature Konstant 1. This is a Temp constant for the Gaussian P vs T function.

$SaTk2 = 0.002$

DOCUMENT: *Spartina alterniflora* Temperature Konstant 2. This is a Temp constant for the Gaussian P vs T function.

SaTopt = 20

DOCUMENT: Spartina alterniflora Optimum Temperature. This is the ideal temperature for Sa production, etc. Set at 20 degC.

Sa_Glim = IF (PARo > 0.0)

THEN (IF (SaRRVvS>SaPvI) THEN (SaRRVvS) ELSE (SaPvI))

ELSE (0.0)

DOCUMENT: Spartina alterniflora Growth Limitation. (unitless). A function that chooses between light and nutrient limitation.

SRRCNFB = MIN(MAX(SaRRCN-SaRRminCN,0.0)/(SaRRmaxCN-SaRRminCN),1.0)

DOCUMENT: Spartina alterniflora RR Nitrogen Feedback. This is a feedback limitation term based upon RR actual, min, and max nitrogen contents (gN/m²). The term is unitless.

SSCNFB = MIN(MAX(SaSHCN-SaSHminCN,0.0)/(SaSHmaxCN-SaSHminCN),1.0)

DOCUMENT: Spartina alterniflora Shoot Nitrogen Feedback. (unitless). This is a Weigert-Wetzel feedback term for Spalt shoot N production.

VITA

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